Riverscape heterogeneity controls on spatial patterns in fish assemblages

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For Dad,

Your lifelong enthusiasm for rivers and conservation is an inspiration

and has led me to be where I am today.

and for Dale,

Without your support, encouragement, tolerance, and unwavering belief in me,

this would not have been possible

Contents

Abstract

Given the importance of spatial heterogeneity in altering dispersal, interspecific interactions, and population persistence, high rates of habitat homogenisation across the globe are a concern. In river networks, confluences and water abstractions likely produce discontinuities in physical conditions, potentially creating hotspots of heterogeneity that influence fish assemblages, including interactions between native and invasive fish. However, mechanisms driving fish assemblage responses to such spatial heterogeneity are not well understood. I investigated how the spatial configuration of flow disturbance around confluences influenced spatial and temporal patterns in fish assemblages, and evaluated the impact of spatial heterogeneity associated with surface water abstractions on fish assemblage structure.

Electrofishing in mainstem and tributary branches of replicate confluences revealed highly context-dependent distributions, contingent upon the combination of flood disturbance history in branches, distance to the confluence and the direction of flow. Shifts in native–invasive species relative abundance were determined by preference of large predatory salmonids for more hydrologically stable conditions, resulting in higher native fish abundance in flood-prone conditions. Distance from confluence effects were stronger upstream than downstream, suggesting flow direction had influenced dispersal. Heterogeneity-related dynamics in fish assemblages meant confluences with homogenous flow conditions had lower fish abundance and higher temporal variability in the relative abundance of native and invasive species than confluences with heterogeneous flow conditions. Evenness scores differed downstream of confluences, with higher assemblage evenness downstream of heterogeneous confluences. These results demonstrate how flow- regime effects are spatially transferred at confluences, creating areas of influential riverscape heterogeneity.

Field surveys and stable isotope analysis revealed reduced flows downstream of abstraction points resulted in significantly lower fish abundances per metre of stream length, higher proportions of native species, shallower mass-abundance relationship slopes and shorter stable isotope-derived food-chain lengths due to the loss of larger fish sizes. Spatial heterogeneity in stream flow associated with water abstractions can therefore alter both the structure and composition of stream fish assemblages, and modify the outcomes of native–invasive species interactions. Overall, my research indicates understanding the role of heterogeneity will assist in identifying locations of ecological significance in river networks and improve the strategic management of fish assemblages, especially in invaded riverscapes.

Frontispiece: The Waimakariri River in the South Island of New Zealand, looking upstream towards the Hawdon River confluence.

Photo: Nixie Boddy

Chapter One:

Introduction

Freshwater ecosystems are among the most globally threatened ecosystems due to losses in biodiversity attributable to increasing anthropogenic pressures (MEA, 2005; Dudgeon *et al.*, 2006; Pittock, Hansen & Abell, 2008). Anthropogenic land-use change, channelization, water impoundment and water abstraction are all major threats to global biodiversity in freshwater systems and have the potential to homogenise riverscapes (MEA, 2005; Dudgeon *et al.*, 2006). Furthermore, habitat homogenisation, through loss of variability in abiotic characteristics across catchments, is one of the primary drivers of recent changes in the diversity and abundance of aquatic biota (Zeni & Casatti, 2014). Therefore, to effectively manage freshwater systems in the face of land-use intensification and climate warming, an understanding of the importance of riverscape-scale changes in the amount and configuration of abiotic heterogeneity is required.

The riverscapes approach is extremely important in freshwater ecology, allowing for the inclusion of spatial heterogeneity and network configuration in the study of freshwater systems and assemblages (Fausch *et al.*, 2002). Vannote (1991) instigated this line of thought through development of the Riverscape Continuum Concept, which proposed a linear gradient of abiotic conditions and biotic communities, related to stream order, from headwaters to the sea. The Serial Discontinuity Concept (Ward & Stanford, 1983) built on this, suggesting impoundments disrupt longitudinal processes and create patchy environmental heterogeneity along the stream profile. The Link Discontinuity Concept (Rice, Greenwood & Joyce, 2001) acknowledged the influence of tributaries on longitudinal processes and the importance of their arrangement, and Fausch *et al.* (2002) included spatial heterogeneity and network configuration

in studies of aquatic assemblages at large spatial scales. The Network Dynamics Hypothesis (Benda *et al.,* 2004) highlighted abrupt changes in physical habitat structure at confluences, and proposed that effects depended on basin shape, size, drainage density and geometry. Kiffney *et al.* (2006) built further on this, suggesting habitat complexity, productivity and abundance of organisms in mainstem rivers peaks at or below tributary junctions. Finally, Milesi & Melo (2014) proposed the effects of tributaries on aquatic assemblages in mainstems depends on the tributary:mainstem size ratio.

Research at the scale of river networks, examining relationships between network components, is becoming progressively more common (Peterson & Ver Hoef, 2010; Flitcroft *et al.*, 2012; Heasley, Clifford & Millington, 2018). Consequently, the ability to identify characteristics of network structure and quantify their importance for ecological processes in stream systems will be very important in determining the value of spatial heterogeneity in the face of increasing broad-scale homogenisation.

Riverscape heterogeneity

Understanding the importance of environmental heterogeneity for diversity and abundance of species is an active area of ecological research (Cromsigt, Prins & Olff, 2009; Smith & Mather, 2013; Hovick *et al.*, 2016; Peláez, Azevedo & Pavanelli, 2017). Environmental heterogeneity often results in patchy species distributions by influencing the availability and distribution of refugia (Magalhães *et al.*, 2002), food (Cromsigt, Prins & Olff, 2009) and reproductive habitat (Ficetola & De Bernardi, 2005). Although small-scale environmental heterogeneity in river networks has been positively related to diversity and abundance of fish species (Fernandes, Podos & Lundberg, 2004; Smith & Mather, 2013; Peláez, Azevedo & Pavanelli, 2017), the role of larger-scale spatial heterogeneity in abiotic conditions in determining aquatic community composition is poorly understood (Kiffney *et al.*, 2006; Rice, 2017). In aquatic

systems, discontinuities, both natural (e.g. confluences) and anthropogenic (e.g. dams and diversions), can create 'hotspots' of heterogeneity in physical conditions that can produce spatially and temporally variable dynamics in resident community structure (Benda *et al.*, 2004; Kiffney *et al.*, 2006; Kennedy *et al.*, 2016). Moreover, whether a particular confluence or diversion creates a 'hotspot' of heterogeneity in the riverscape or not, may depend on the spatial arrangement of habitat types (Cathcart *et al.*, 2018). Most research of confluence environments has focussed on local-scale heterogeneity, particularly downstream of the confluence (Rice, Greenwood & Joyce, 2001; Kiffney *et al.*, 2006; Milesi & Melo, 2014), without specifically investigating the potential role of confluences in providing heterogeneity at the riverscape-scale.

Spatially variable flow disturbance in stream networks is an important component of riverscape heterogeneity (Bunn & Arthington, 2002; Benda *et al.*, 2004), and could be a particularly important driver of configuration-dependent dynamics in aquatic communities. The effect of heterogeneity in river flow regimes on aquatic biodiversity and abundance has been studied at small spatial scales (Brown, Hannah & Milner, 2007; Garcia, Schnauder & Pusch, 2012), however little is known about how spatial heterogeneity interacts with fish assemblage composition at larger scales. Consequently, understanding the influence of spatial heterogeneity in stream flow characteristics on the structure and abundance of freshwater fish assemblages will advance freshwater ecology and provide information to underpin aquatic conservation decisions in the face of ongoing global change.

Defining heterogeneity in flow disturbance

While classic hydrological variables such as flood magnitude, frequency and duration are effective measures of flow variability, they do not necessarily reflect the disturbance experienced by local stream organisms, which can be influenced by factors such as reach

geomorphology (Peckarsky et al. 2014). Because the native galaxiid fishes and the invertebrates fed on by galaxiids and trout in these streams are benthic, I wanted to characterise 'flow disturbance' using a metric relevant to the local community. Streambed instability is a good measure of physical flooding disturbance to benthic organisms in streams (Matthaei et al. 2000; Jellyman et al. 2013; Peckarsky et al. 2014), so here I define disturbance as flood events that affect the stream bed, both through removal of organisms or by altering physical habitat (Peckarsky et al. 2014). The RDI index is a simple and effective way to characterise benthic stability, using evidence of hydraulic and geomorphological disturbance, and has been found to be a reliable assessment of stream channel stability when the same observer is used across sites (Peckarsky et al. 2014). Therefore in this thesis, the RDI index is used as a measure of 'flow disturbance' as experienced by freshwater fish in these river networks.

Fish assemblage composition

Our knowledge of broad-scale patterns of community assembly has greatly increased with the recent shift from focussing on locally-interacting species in isolated communities to highly spatially and temporally connected metacommunities (Leibold *et al.*, 2004; Chisholm, Lindo & Gonzalez, 2011; Logue *et al.*, 2011). The combined influences of local hydrological characteristics and the regional species pool are primary determinants of local richness in freshwater fish (Niu, Franczyk & Knouft, 2012). However, due to source–sink population dynamics, use of refugia, dispersal, and recolonisation after disturbance events (Fausch *et al.*, 2002; Campbell Grant, Lowe & Fagan, 2007), it is likely that the diversity and abundance of fish at a particular site could also be related to riverscape heterogeneity. Therefore, if riverscape-scale heterogeneity in flow characteristics influences these community assembly processes, it is also likely to play a major role in the spatial and temporal stability of fish populations.

Invasions in heterogeneous landscapes

Biological invasions have strong negative effects on native species worldwide (Vitousek *et al.*, 1996; Clavero & Garcı´a-Berthou, 2005; Maciel & Lutscher, 2018). However, their effects are disproportionately severe in freshwater ecosystems (Moorhouse & Macdonald, 2014), making understanding factors mediating their influence extremely important. Most biological invasions occur in heterogeneous environments (Maciel & Lutscher, 2018), so environmental heterogeneity and invasive species are likely to interact to influence native species assemblages (Vander Zanden, Hansen & Latzka, 2017). Moreover, interspecific interactions such as these are fundamental processes structuring many ecological communities, but knowledge of their spatial and temporal variability is still poor (Poisot, Stouffer & Gravel, 2015). Therefore, to better understand how invasive species and spatial heterogeneity in river networks interact to influence fish assemblages, more empirical studies are required.

The New Zealand context

Salmonid fishes are one of the most widespread invaders in the world, and their impact on native fish assemblages are a major concern (Fausch, 1988; Lowe *et al.*, 2000; McIntosh, McHugh & Budy, 2012; Hasegawa, Mori & Yamazaki, 2016; Morita, 2018). Many native fish declines have been blamed on competitive displacement and predation by introduced trout, such as the crisis facing Galaxiidae in the Southern Hemisphere (McDowall, 2006; Habit *et al.*, 2010; McIntosh *et al.*, 2010; Jones & Closs, 2015; Sowersby, Thompson & Wong, 2015). A very high proportion of native freshwater fish in New Zealand are classified as threatened or declining (McDowall, 2006), for example, in the Galaxiidae family, 81% of species are ranked as threatened or at risk (Goodman *et al.*, 2014). Because New Zealand has both a highly variable climate, which creates river networks with highly spatially heterogeneous flow regimes, and invasive trout (McIntosh, 2000), it is an ideal study system for investigating the

likely interacting influences of heterogeneity and invasive species on freshwater fish assemblages. The abundance and distribution of galaxiids is usually negatively affected by competition and predation from trout, which often leads to their exclusion (McIntosh *et al.*, 2010). However, because trout have strong habitat preferences and are negatively influenced by physical habitat conditions like flooding (Fausch *et al.*, 2001; Budy *et al.*, 2008; Jellyman *et al.*, 2017), it is likely that spatial heterogeneity in flow disturbance will impact the outcome of native–invasive interactions, and consequently influence the relative abundance of native galaxiids and introduced trout at a site.

Thesis structure

In this thesis I focus on the relationship between spatial heterogeneity in flow conditions and spatial and temporal shifts in fish assemblage structure and abundance in invaded riverscapes in New Zealand.

In Chapter Two, I used a spatially nested survey design to investigate the roles of the presence and configuration of heterogeneity in flood disturbance conditions around confluences in influencing fish abundance and community evenness in the Canterbury High Country, South Island of New Zealand. The survey contrasted confluences with different configurations of tributary and mainstem flow disturbance regimes to evaluate spatial patterns in fish assemblages in the tributary, upstream mainstem, and downstream mainstem branches. I predicted the layout of flow disturbance conditions around confluences would influence the presence and configuration of spatial heterogeneity, and strongly influence spatial patterns in fish assemblage abundance and evenness.

I determined during the survey described in Chapter Two that spatial patterns in fish assemblages, particularly the abundances of native Galaxidae and non-native Salmonidae, varied with distance from the confluence. Therefore, in Chapter Three I investigated spatial

patterns in the relative abundance of native and invasive species associated with the configuration of flood disturbance around confluences, and how they changed relative to proximity and flow direction to the confluence.

Because I observed such strong patterns in fish communities associated with heterogeneity in flow regimes around confluences while conducting the field survey for Chapters Two and Three, I wondered if the inherent presence of heterogeneity in flow regimes, regardless of spatial configuration, was enough to produce significant spatial and temporal differences in fish assemblages. Thus, in Chapter Four, using temporal surveys with the same survey design described in Chapter Two, I investigated the influence of the spatial juxtaposition of disparate flow disturbance regimes around confluences on fish abundance and temporal stability in assemblage composition. I predicted higher spatial heterogeneity in flow conditions around confluences would produce higher overall fish abundances and more temporally stable native–invasive species interactions. During this temporal survey I determined that fish assemblages were responsive to spatial variation in flow regime, and postulated that variation in flow regime in response to anthropogenic water abstraction may also influence spatial patterns in fish assemblages.

In Chapter Five, therefore, I investigated how anthropogenically-derived spatial heterogeneity in stream flow influenced fish assemblage structure. Surveys and stable isotope analysis were used to evaluate the impact of differing levels of flow abstraction on fish assemblage structure, and native–invasive patterns of coexistence, associated with small surface water abstractions in the Canterbury region of New Zealand. For this, a nested longitudinal study design was used to separate longitudinal shifts in fish assemblages from those associated with surface water abstractions.

Finally, in Chapter Six I integrate and discuss findings from Chapters Two–Five. Specifically, how influences of spatial heterogeneity in flow regimes both naturally, associated with confluences, and artificially, resulting from surface water abstractions, can influence spatial and temporal patterns in stream fish assemblages in invaded riverscapes. Finally, I review implications of my research, highlighting the importance of spatial heterogeneity in invaded riverscapes to conservation managers.

This thesis has been written as a series of four stand-alone scientific papers intended for publication (Chapters Two–Five). As a result there is some necessary repetition in the introduction and methods sections. While all chapters were multi-authored, the writing and analysis were primarily mine, with the exception of Chapter Five which was equally co-authored with Kevin Fraley, a fellow PhD student. Contributions of additional authors have been noted in the acknowledgements section. Figures and tables are included within each chapter, with one numbering system running throughout the entire thesis. All references are provided at the end of the thesis to avoid repetition.

Plate 1. Example of spatial heterogeneity in flow disturbance between two rivers at a confluence of a stable spring-fed river (left) and a flood-disturbed river (right), on the Waimakariri River Floodplain.

Photo: Nixie Boddy

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Chapter Two "Confluence configuration of river networks controls spatial patterns in fish communities"

Boddy, N.C., Booker, D.J., and A.R. McIntosh. Confluence configuration of river networks controls spatial patterns in fish communities.

Submitted to Landscape Ecology 15/3/2018, currently in review.

Please detail the nature and extent (%) of contribution by the candidate:

Nixie was responsible for the study design, field work, statistical analysis, and writing for this manuscript (80%).

Certification by Co-authors:

If there is more than one co-author then a single co-author can sign on behalf of all

The undersigned certifies that:

- The above statement correctly reflects the nature and extent of the PhD candidate's contribution to this co-authored work
- In cases where the candidate was the lead author of the co-authored work he or she wrote the text

Name: *Angus McIntosh* Signature:  Date: *28/6/2018*

Chapter Two:

Confluence configuration of river networks controls spatial patterns in fish communities

Introduction

Spatial heterogeneity is a critical element of all ecosystems, with the ability to alter ecological processes such as the movement of organisms and outcomes of interspecific interactions (Pickett & Cadenasso, 1995; Scheiner & Willig, 2008). Environmental heterogeneity often results in patchy species distributions by influencing, for example, the availability and distribution of refugia (Magalhães *et al.*, 2002), food (Cromsigt, Prins & Olff, 2009) and habitat suitable for reproduction (Ficetola & De Bernardi, 2005). Landscape-scale habitat homogenisation, through loss of variability in abiotic characteristics predominantly via land-use change, channelization, water impoundment and water abstraction, has made freshwater systems among the most highly threatened in the world (MEA, 2005; Dudgeon *et al.*, 2006; Zeni & Casatti, 2014). Moreover, the hierarchically-organised spatial structure of riverscapes, overlaid with strong directional connectivity which integrates processes occurring at different spatial scales (McCluney *et al.*, 2014), makes understanding spatial patterns of freshwater communities and their interactions with habitat heterogeneity at riverscape scales especially important.

Quantifying spatial structure in river network communities is the first step to identifying and managing large-scale drivers of structure in riverscapes (Ganio, Torgersen & Gresswell, 2005).

Spatial arrangement of tributaries could be a particularly influential factor in the longitudinal organisation of freshwater biota (Rice, Greenwood & Joyce, 2001), because each confluence has the potential to disrupt the longitudinal continuum through changes in water volume, substrate size, water quality, channel hydraulics, flow and thermal regimes (Rice, Greenwood & Joyce, 2001; Benda *et al.*, 2004). Moreover, there is potential for abiotic influences in one branch to be transferred upstream and downstream to other branches in the confluence via biotic communities and associated biotic interactions which are connected through the river network. Thus, the spatial layout of tributary branches, and their abiotic conditions, is likely to be an important determinant of riverine processes through their influence on the presence and configuration of spatial heterogeneity. However, studies of stream network configuration effects on communities, and particularly the transfer of influence among branches, are rare (Campbell Grant, Lowe & Fagan, 2007; Flitcroft *et al.*, 2012).

Disturbance within a stream network, through high flow variability and ability to cause physical disturbance during flooding, is an important component of riverscape heterogeneity and could be a particularly important driver of such configuration-dependent dynamics. The branching hierarchy of river networks interacts with catchment disturbances such as floods to spatially organise the distribution of riverine habitat in a highly non-uniform way (Benda *et al.*, 2004). Fluctuations in stream flow are the primary form of environmental variability in riverine ecosystems, both due to their role in physical habitat modification and influences on community composition through effects on mortality and recruitment processes (Grossman *et al.*, 1998; Jackson, Peres-Neto & Olden, 2001). The effects of spatially heterogeneous flow disturbance regimes in aquatic systems have been evaluated in the context of aquatic invertebrates (Brown, Hannah & Milner, 2007; Garcia, Schnauder & Pusch, 2012; Milesi & Melo, 2014), however little is known about impacts on fish community composition patterns, or the potential role of spatially transferred influence in aquatic systems. Although local hydrological characteristics

and the regional species pool are primary determinants of local richness in riverine fish (Niu, Franczyk & Knouft, 2012), due to source sink-population dynamics, use of refugia, dispersal, and recolonisation after disturbance events, it is likely that the fish community at a particular site could also be related to the configuration of nearby confluences and the conditions and fish population therein. Therefore, understanding how the configuration of conditions around confluences influences fish communities in rivers should be insightful.

I investigated the importance of the configuration of flow disturbance regimes around confluences for spatial patterns in fish abundance and evenness in natural riverscapes in New Zealand. While species richness continues to be the most common measure of biodiversity, issues with bias resulting from differing species detectability frequently complicates hypothesis testing (Brose, Martinez & Williams, 2003). Estimates of evenness, in contrast, are more robust even when based on few samples, therefore abundance and evenness were used as my fish community response metrics (Brose, Martinez & Williams, 2003). Riverscape-scale patchiness in flow regimes is likely to be a very important driver of aquatic community patterns, however it is difficult to sample at that scale without losing data resolution or impacting fieldwork feasibility. Confluences represent hotspots of riverscape-scale heterogeneity that are feasible to sample at an intermediate scale to examine larger-scale patterns and processes. At each confluence I studied there were three 'branches' sampled: (1) upstream mainstem, (2) tributary and (3) downstream mainstem. I created confluence configuration categories to include the juxtaposition of different abiotic conditions, particularly physical disturbance associated with flooding as measured by the Pfankuch river disturbance index (Fig. 2.1). These confluence configurations included: (a) confluences between two 'stable' streams, (b) confluences between a 'stable' mainstem and a 'disturbed' tributary, (c) confluences with a 'disturbed' mainstem and a 'stable' tributary, and finally (d) confluences between two streams with 'disturbed' flow regimes. This study design enabled me to examine both the importance of stream branch

juxtaposition, and the role of spatial position in the confluence in influencing fish community evenness and abundance. I hypothesised that confluence configuration and branch would interact to produce highly spatially variable patterns in fish abundance (H1) and fish community evenness (H2). In addition, I hypothesised that the presence of tributaries with different abiotic conditions compared to the mainstem river would increase fish abundance (H3) and evenness (H4), compared to confluences containing two stream branches with similar physical characteristics.

Methods

Field survey

I surveyed twelve confluences in the Canterbury high country, New Zealand. The presence of both large braided river floodplains in this area creating stable spring systems juxtaposed with highly flood-disturbed braided river channels, and springs associated with limestone in otherwise steep eroded catchments, made this a perfect environment for this research (Fig. 1). The confluences included in this study were a good representation of those present in the region. Confluences were selected to incorporate the four different combinations of flow disturbance regimes mentioned previously (‘confluence configuration’), and to be, where possible, junctions between third order mainstems and second order tributaries to control for the effects of stream size. Confluences were classified into the categories (a-d) using available information, including flow characteristics collected during initial site visits (Fig. 2.1).

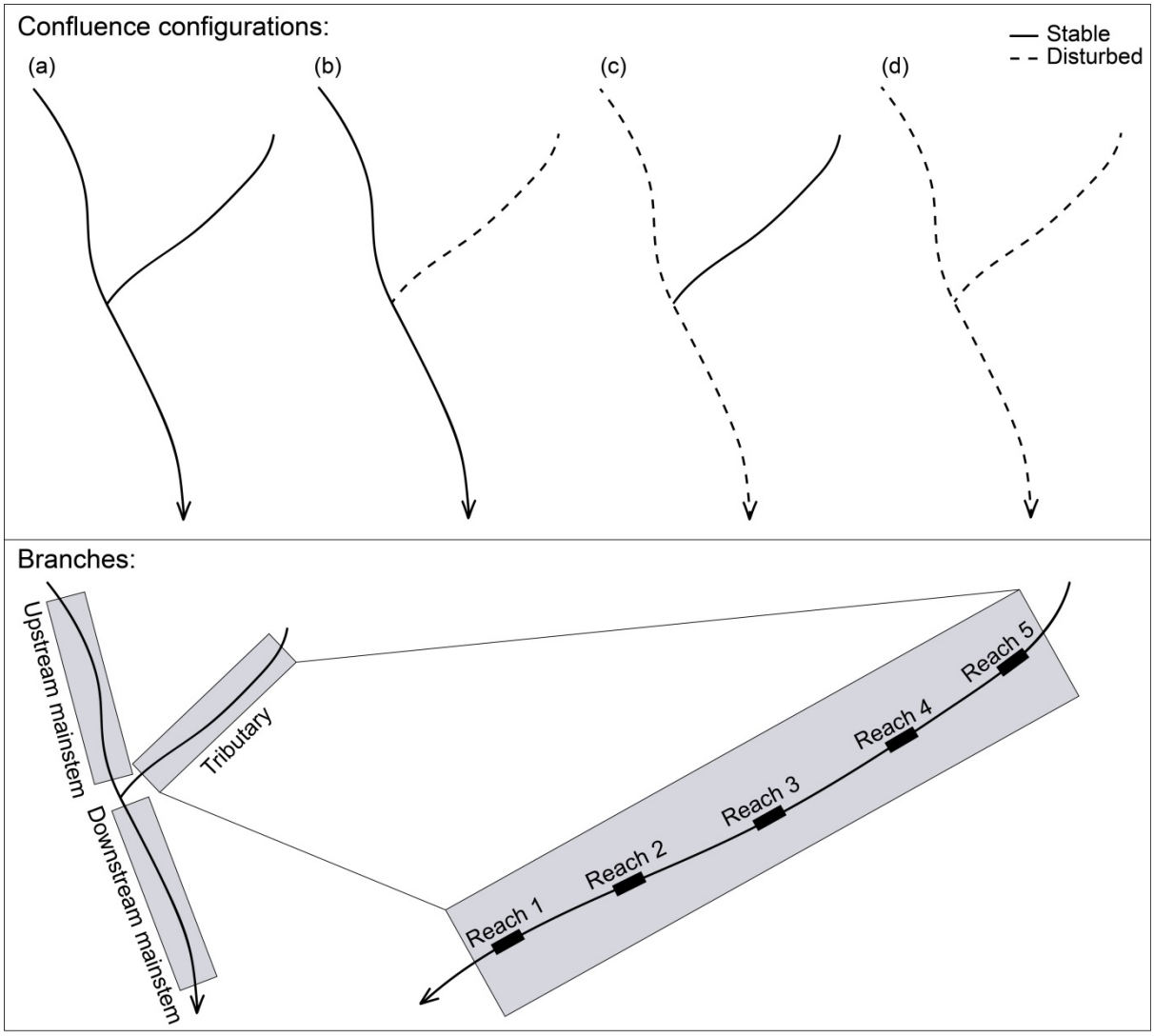

Fig. 2.1: Field sampling design showing the four confluence configurations (upper panel) based on the combination of stable and disturbed flow regimes (solid and dashed lines respectively) within the three 'branches,' and the arrangement of sampling reaches within a branch (lower panel). 'Stable' streams had low flood disturbance, and 'disturbed' streams had high flood disturbance. Confluence configurations were (a)'stable-stable' (both mainstem and tributary classed as stable), (b)'stable-disturbed' (stable mainstem and disturbed tributary), (c)'disturbed-stable' (disturbed mainstem and stable tributary) and (d)'disturbed-disturbed' (both mainstem and tributary classed as disturbed), and each confluence involved three 'branches:' the tributary, upstream mainstem, downstream mainstem. Within each branch, five reaches were sampled, making a total of 15 sampling reaches per confluence.

Each confluence survey involved sampling three 'branches' (Fig. 2.1). To ensure I sampled at an appropriate scale to resolve the spatial patterns of mobile species, I sampled five 'reaches' in each branch, making a total of 15 sampling reaches per confluence (Fig. 2.1). Sampling reach length was five times the stream width, and the distance between reaches was five times the average reach length for that branch. The reach sampled nearest the confluence began one reach length from the confluence, so the distance sampled for each branch was 130 times the stream width from the confluence. Sampling reach length was a constant multiple of the stream width (averaged over all five reaches in a branch) to avoid incorporating variability due to sampling different proportions of the available habitat depending on stream size (Peterson & Ver Hoef, 2010). Moreover, five stream widths was sufficient to represent the habitat complexity in the smaller streams, and not so large that it was unachievable to sample reaches in larger rivers (>10 m wide) in a day. Each sampling reach was single-pass electrofished in an upstream direction without stopnets, and fish caught were identified to species.

Single-upstream-pass electrofishing is useful for assessing fish abundance and assemblage structure in small streams (Simonson & Lyons, 1995), but to ensure this was a valid sampling approach for my system I also quantitatively electrofished eight 30-m reaches using three-pass electrofishing with stopnets; this sampling method is typically applied to evaluate the probability of detecting fish species and the precision of single-pass electrofishing abundance estimates (McIntosh, Crowl & Townsend, 1994; Boddy & McIntosh, 2017). At each three-pass site, a 30-m reach was delineated with stopnets at the top and bottom of the reach. Single-pass electrofishing, as described above with reaches five times the stream width, was then conducted in the centre of the 30-m netted reach, followed by three to four runs of depletion sampling in the reach to estimate total diversity and abundance of all species present. Time

spent electrofishing was recorded to ensure consistency of sampling effort between sites (Dauwalter & Pert, 2003).

Electrofishing was undertaken using a Kainga EFM 300 backpack electrofisher (NIWA Instrument Systems, New Zealand) generating 400 – 600V of pulsed direct current. Electrofishing was conducted in a downstream direction into a pushnet, the standard practice for sampling fish communities dominated by trout and galaxiids in New Zealand streams (Townsend & Crowl, 1991). To measure spatial and temporal variation in water temperature I installed a logger (Onset HOBO pendant) in every branch of each sampled confluence (total of 36 temperature loggers), to record hourly temperature measurements for the duration of the 2014 – 15 austral summer, which the electrofishing was conducted at the end of. To detect finer scale temperature variation, spot temperature measurements were taken at every sampling reach at least four times during the summer. The HOBO logger data were used, with calibration from spot temperature measurements, to create temperature metrics for each reach, including average daily temperature, maximum daily temperature, average daily temperature range, and maximum daily temperature range.

To quantify flow disturbance in confluence branches I used the Pfankuch River Disturbance Index (RDI) which combines visual estimates of 15 aspects of channel morphology including indicators from both the stream bed and banks to evaluate physical stability of a river channel (Pfankuch, 1975; McHugh, McIntosh & Jellyman, 2010; Jellyman, Booker & McIntosh, 2013). Each site was scored by the same observer to maximise between-site consistency. Additional abiotic habitat variables were measured at every sampling reach, including: substrate size, water depth and velocity (three cross-sections per reach, six measurements per cross-section), wetted stream width, macrophyte cover, basic water chemistry (pH, dissolved oxygen and conductivity), and reach flow characteristics; percent of reach consisting of

cascades, riffles, runs, and pools (Leathwick *et al.*, 2008; Boddy & McIntosh, 2017). Macrophyte cover and percent of reach with different flow characteristics were visually estimated and mean substrate sizes were obtained using a Wolman Walk to select 50 random substrate particles for measurement of the beta axis (Green, 2003). I assessed the four confluence configuration categories using these measured habitat variables.

Statistical analysis

All analysis was conducted in R (R Development Core Team, 2016). RDI was intended to be used as a continuous variable in this study, however we were unable to find streams spanning the mid-range of RDI scores, thus we used RDI score was used to characterise each branch as either "stable" (RDI < 100) or "disturbed" (RDI >100). Principal components analysis (PCA), graphed using the lattice package (Sarkar, 2008), was used to investigate covariance between RDI and other abiotic habitat characteristics and to give a physical description of the confluences. This PCA was also used in conjunction with PERMANOVA (Oksanen *et al.*, 2017) to assess if physical site characteristics differed significantly depending on branch and confluence configuration. The precision of single-pass upstream electrofishing was assessed using linear regression against the quantitative three-pass electrofishing technique with stopnets. Fish community responses were total fish abundance and fish community evenness (i.e., how numerically equal species abundances were).

Generalised linear mixed-effects models, created in lme4 (Bates *et al.*, 2015), were used to test for an interaction between confluence configuration category (i.e., stable-stable, disturbed-disturbed, stable-disturbed and disturbed-stable), and branch (i.e., tributary, upstream and downstream mainstem) on fish abundance and evenness. ANOVAs were used to compare between models with and without the interaction term to determine its significance. These models had Poisson and Gaussian error distributions for abundance and evenness, respectively.

I included branch and distance to confluence as a fixed effect, and confluence identity as a random effect. To evaluate potential spatial autocorrelation between reaches due to the nested nature of the study design, I created a spatial autocorrelation structure using Manhattan distances along each branch to include network distances between each pair of sites for each confluence. I then compared models with and without the spatial autocorrelation parameter using model outputs and AIC_c scores for small sample sizes to evaluate justification for inclusion in the following analysis.

Marginal and conditional coefficients of determination (Nakagawa & Schielzeth, 2013) were used to assess model fit and were calculated with the MumIn package (Barton, 2016). R^2 marginal (R^2m) expresses absolute model fit including only the fixed effects, while R^2conditional (R^2c) expresses model fit including both fixed and random effects. Because confluence identity was a random effect in my model (i.e., which of the twelve confluences the reach in question was from), comparing the R^2m and R^2c values allowed the importance of confluence-specific effects in explaining variability in the data to be evaluated. Graphs of the glmer model results were produced using the ggplot2 (Wickham, 2009) and effects (Fox, 2003) packages.

Results

Defining confluence configurations

My disturbance measure, RDI score, was the primary driver of the first principal component axis which explained 49% of the variation in physical characteristics between sites (Fig. 2.2). This supported the use of RDI scores in broadly categorising stream branches into ‘stable’ (RDI score < 100, low flow disturbance e.g. spring fed streams) and ‘disturbed’ (RDI > 100, high flow disturbance e.g. braided river). Stream temperature, evaluated across a range of tested

metrics, including average daily temperature, maximum temperature, average daily temperature range and maximum daily temperature range, had a relatively minor influence on the PCA axes (Fig. 2.2a). RDI was weakly positively correlated with average daily stream temperature and stream width, and was not correlated with elevation, mean substrate size or percent riffle or run.

PERMANOVA results showed branch-related patterns in abiotic habitat characteristics differed significantly depending on confluence configuration (R^2 = 0.1, df = 6, 24, p=0.001). Differences across the four confluence configurations were driven by the disturbance axis, where stable reaches had low axis one scores, and disturbed reaches had high axis one scores (Figs. 2.2b-e). Stable-stable and disturbed-disturbed configurations showed no consistent pattern in abiotic conditions associated with branch (Fig.2.2b and 2.2d, respectively) due to small differences between branches within each confluence, but grouped on the left and right of the axis one, respectively. The stable-disturbed configuration had consistently lower axis one scores in upstream reaches than tributary and downstream reaches, likely due to input from the disturbed tributary changing downstream reach disturbance characteristics (Fig. 2.2c). The disturbed-stable confluence configuration had consistently lower axis one scores and plotted further left in the stable tributary reaches, with the upstream and downstream mainstem reaches plotting further right with higher axis one scores (Fig. 2.2e). Interestingly, downstream branches in disturbed-stable configurations were displaced slightly left (lower axis one) than the upstream mainstem reaches, indicating the stable tributaries were having an influence, albeit a small one, on downstream mainstem physical habitat (Fig. 2.2e). Distribution of reaches along principal component axis two showed no pattern across configuration and branch types and reflected variations in the proportions of riffle and run habitat.

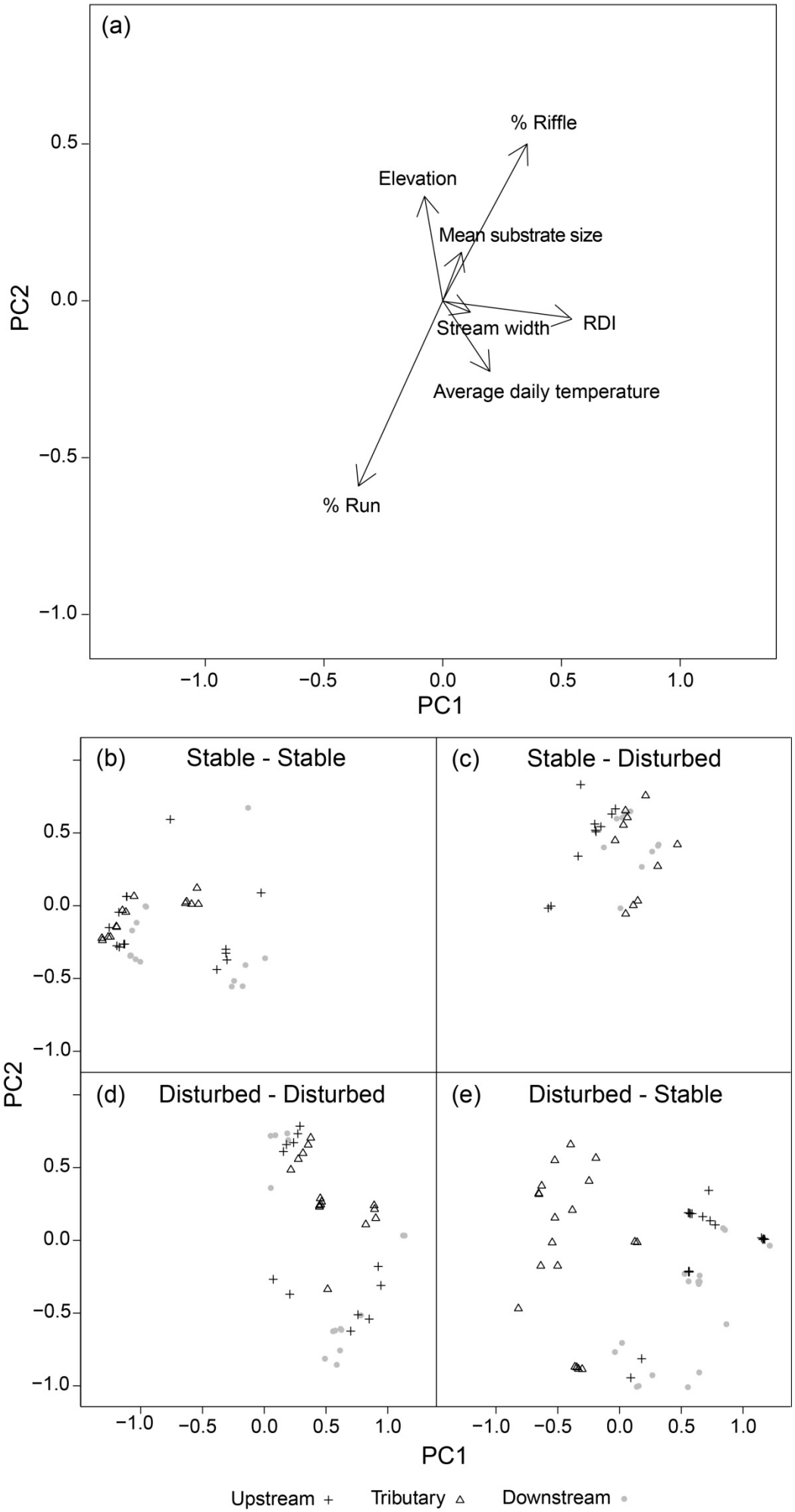
(a)
% Riffle
Elevation
Mean substrate size
RDI
Stream width
Average daily temperature
% Run
PC2
PC1
(b) Stable - Stable
(c) Stable - Disturbed
(d) Disturbed - Disturbed
(e) Disturbed - Stable
Upstream
Tributary
Downstream

Fig. 2.2: Principal Components Analysis of abiotic variables illustrating extent of (a) covariance between RDI (Pfankuch River Disturbance Index) and other physical variables, and (b-e) how abiotic site characteristics differed depending on confluence configuration and branch. Arrow length and direction in (a) show the relative influence and relationships between each of the seven most influential abiotic habitat variables: RDI, average daily temperature (average of hourly temperature measurement recorded over the 2014-15 summer), mean substrate size (the average of 50 substrate particles measured using the Wolman Walk), stream width (mean width in each reach), elevation (m) and % riffle and run (percent of reach consisting of cascades, riffles, runs, and pools). Panels b-e show individual reach locations within ordination space, categorised by confluence configuration. Reaches with RDI scores >100 were classified as 'disturbed,' and reaches <100 were classified as 'stable.' 'Stable-Stable' (b) represents confluences between two stable streams, and 'Stable-Disturbed' (c) represents confluences with a stable mainstem and a disturbed tributary. 'Disturbed-Disturbed' (d) represents confluences between two disturbed streams, and 'Disturbed-Stable' (e) configurations are confluences with disturbed mainstems and stable tributaries. Crosses represent reaches upstream of the confluence, triangles are tributary reaches, and circles are mainstem reaches downstream of the confluence.

Qualitative electrofishing method

Of the seven fish species encountered, five were native: alpine galaxias (*Galaxias paucispondylus*), Canterbury galaxias (*Galaxias vulgaris*), kōaro (*Galaxias brevipinnis*), longfin eels (*Anguilla dieffenbachii*) and upland bullies (*Gobiomorphus breviceps*). The remaining two were non-native salmonids: brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*).

In the eight reaches where the effectiveness of the single-pass upstream electrofishing was compared to the 30-m three-pass technique, the single upstream pass method correlated well for Galaxiidae (R^2 = 0.99) and Salmonidae abundance (R^2 = 0.82), but was a less precise measure of overall fish diversity (R^2 = 0.63). Due to salmoniids and galaxiids making up 98.6% of total fish abundance on average, and 100% of total fish abundance at 91% of the sampled reaches, single-pass upstream electrofishing was deemed suitable for measuring overall fish abundance and community evenness. The poorer ability of the single upstream pass method to represent overall fish richness likely reflects low species richness in the system (seven species were encountered in total, with a maximum of four in a reach), limiting my strength of inference for fish diversity, thus this response was not evaluated in this study.

Model structure

As a main effect in the analysis, distance to confluence was not a significant predictor of fish community evenness (F=1.74, df=1, p=0.17). It was however a significant predictor of fish community abundance (F=21.39, df=1, p<0.0001), but had poor explanatory power at the fish community level; marginal R^2 increased from 0.16 to 0.165, and conditional R^2 from 0.316 to 0.318 with its inclusion. The inclusion of spatial autocorrelation using Manhattan distances was not supported in any of my models, with identical model outputs, no increase in predictive performance, and elevated AIC_c scores for both response variables. This suggested my model format sufficiently accounted for the spatial structure of my data, and there were sufficient gaps between reaches for spatial autocorrelation to not compromise inference, therefore it was excluded from my final model. Both sets of models, however, had substantial differences between R^2m and R^2c, suggesting the random effect of confluence identity (i.e., which stream network the reach was in) played an important role in determining fish community composition (Table 2.1).

Table 2.1: Generalised linear mixed-effects model results showing interactions between confluence configuration and branch, and the main effect of distance to confluence on total fish abundance (per metre squared) and fish community evenness in each reach. R^2 marginal (R^2m) expresses absolute model fit including only the fixed effects, while R^2conditional (R^2c) expresses model fit including both fixed and random effects.

Response	Variable	N	df	F-value	p-value	R^2m	R^2c
Total fish abundance	Configuration x Branch	177	6	57.91	<0.001	0.17	0.32
	Distance to confluence	177	1	21.39	<0.001		
Evenness	Configuration x Branch	177	6	2.55	0.017	0.22	0.42
	Distance to confluence	177	1	1.74	0.168		

Fish community analysis

The configuration of abiotic conditions around confluences (confluence configuration) and position of a sampled reach with respect to the confluence (branch) interacted significantly to create configuration-specific patterns in fish community abundance ($F=57.91$, $df=6$, $p<0.001$; Table 2.1), supporting my first hypothesis. Fish abundance was consistently low in upstream mainstem branches across all confluence configurations (Fig. 2.3). In comparison, confluence configuration had a large effect on tributary fish abundance. Disturbed tributaries connected to stable mainstems had much higher fish abundance than disturbed tributaries adjacent to disturbed mainstems, and had much higher abundances than any other tributary branch combination (Fig. 2.3). Fish abundance was higher in stable tributaries juxtaposed with stable mainstems, than in stable tributaries adjoining a disturbed mainstem. Thus, disturbed mainstems were always associated with low tributary abundance, in contrast to disturbed conditions in tributaries juxtaposed with stable mainstems, which had exceptionally high

abundance. Downstream mainstem fish abundance differed little from upstream fish abundance in stable-stable and disturbed-disturbed configurations, but showed a slight increase in disturbed-stable confluences, and a substantial increase in abundance occurred in stable-disturbed configurations compared to the mainstem upstream (Fig.2.3). Importantly, this meant fish abundance was higher, regardless of whether the mainstem was disturbed or stable, if the tributary stream contained a different disturbance regime to the mainstem (Fig. 2.3). I ruled out the possibility of this pattern being driven by edge effects as the significance and spatial patterns in abundance between branches were the same whether fish per metre or fish per metre squared was used as a response. Overall, these patterns suggest heterogeneity in flow disturbance regimes around confluences (disturbed-stable and stable-disturbed) generally produced higher fish abundance downstream of the confluence than homogenous confluences (stable-stable and disturbed-disturbed), supporting hypothesis three.

My second hypothesis, that fish community evenness around confluences depended on an interaction between the configuration of the confluence and branch, was also supported ($F=2.55$, $df=6$, $p=0.017$; Table 2.1). Fish community evenness was not significantly different between configurations regardless of disturbance regime in upstream mainstem and tributary branches (Fig. 2.4). Fish community evenness was similar in disturbed downstream branches regardless of conditions upstream, however stable downstream branches with a disturbed tributary upstream had significantly higher evenness than downstream branches in stable-stable confluence configurations (Fig. 2.4). Overall, significant differences in fish community evenness only occurred between different confluence configuration categories in downstream mainstem branches, and communities were most even in stable downstream reaches with a disturbed tributary, partially supporting hypothesis four.

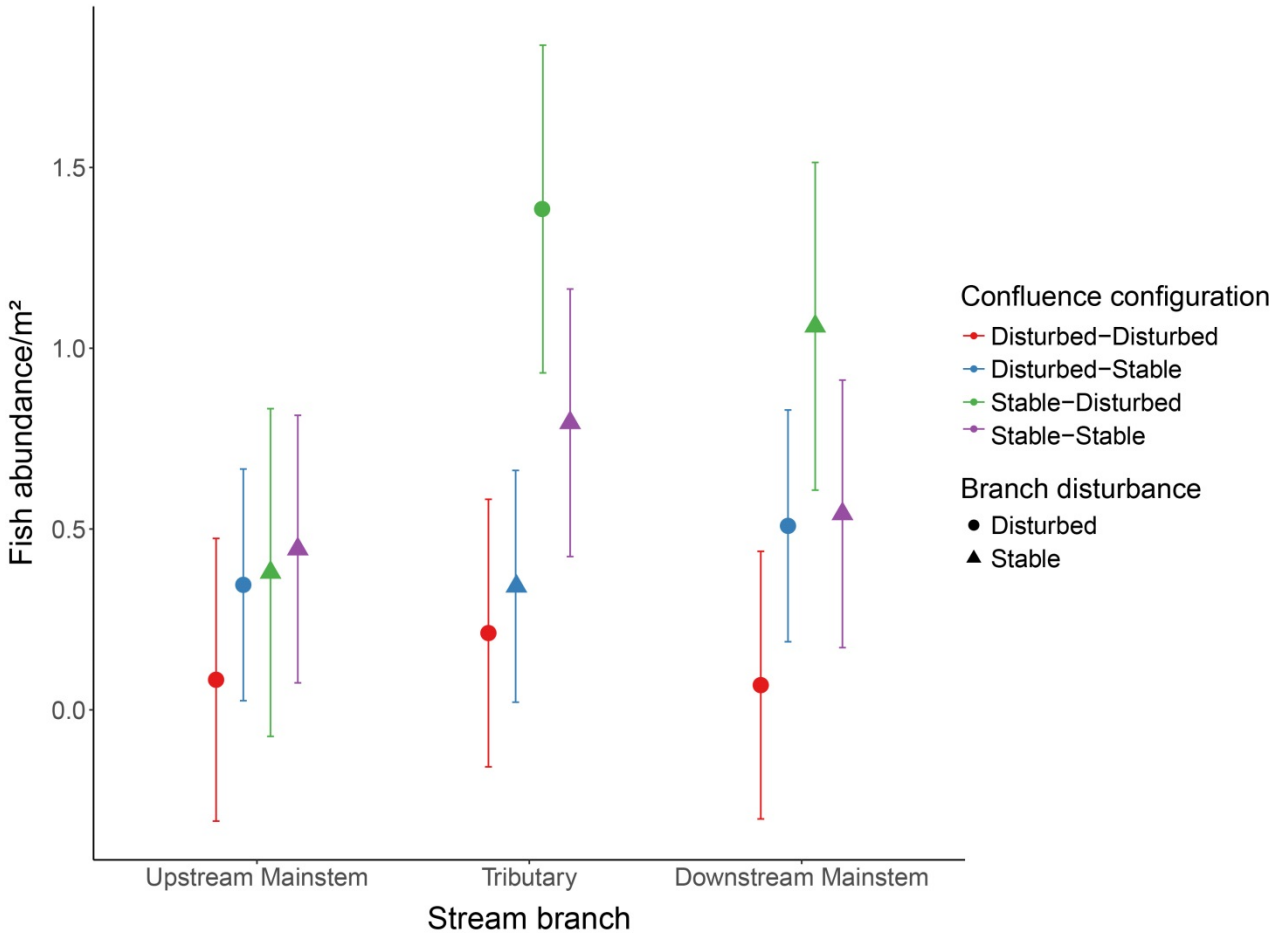

Fig. 2.3: Results from a generalised linear mixed-effects model showing a significant interaction between confluence configuration and branch on total fish abundance per metre squared. Points are model estimates with 95% confidence intervals. Colours represent confluence configuration categories (red, disturbed-disturbed; blue, disturbed-stable; green, stable-disturbed; purple, stable-stable) and shapes represent branch disturbance category (circles, disturbed; triangle, stable).

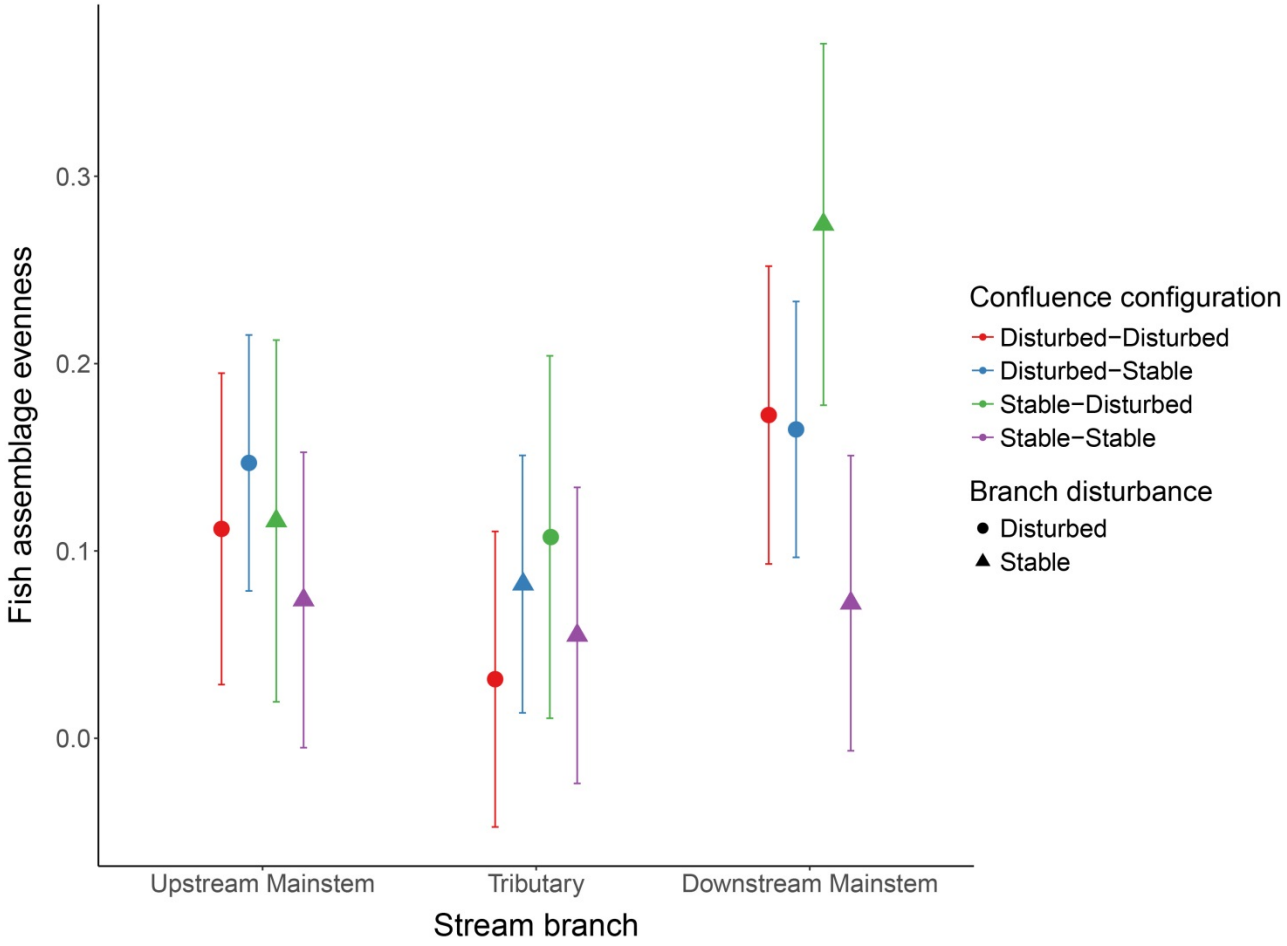

Fig. 2.4: Results from a generalised linear mixed-effects model showing a significant interaction between confluence configuration and branch on fish community evenness in each reach. Points are model estimates with 95% confidence intervals. Colours represent confluence configuration categories (red, disturbed-disturbed; blue, disturbed-stable; green, stable-disturbed; purple, stable-stable) and shapes represent branch disturbance category (circles, disturbed; triangle, stable).

Discussion

Understanding the importance of environmental heterogeneity for diversity and abundance of species is important in the face of increasing habitat homogenisation, especially of aquatic environments (Smith & Mather, 2013; Zeni & Casatti, 2014). Despite the importance of confluences as discontinuities to river continua and potential to be 'hotspots' of heterogeneity, little is known about drivers of fish communities in confluence habitats (Czeglédi *et al.*, 2015). I examined how the configuration of flow disturbance regimes around confluences in a highly diverse flow-disturbed riverscape affected fish abundance and community evenness patterns in stream networks. My results reveal configuration-dependent patterns in fish communities and spatially-transferred influence both upstream and downstream from the confluence, demonstrating the importance of understanding not just the presence of environmental heterogeneity, but its spatial context.

Spatial patterns in fish abundance and evenness differed significantly between confluence branches, depending on the configuration of flow disturbance conditions around the confluence, supporting my first and second hypotheses. These configuration-dependent patterns are not entirely consistent with previous research suggesting fish abundance and diversity peak downstream of tributary confluences predominantly due to increased diversity in habitat structure (Fernandes, Podos & Lundberg, 2004; Kiffney *et al.*, 2006; Hitt & Angermeier, 2008). My results indicate these effects depend on how confluences are configured. The difference in conclusions could be attributed to prior studies not considering variation in habitat characteristics between mainstem and tributary branches (although see Hitt & Angermeier, 2008 who assumed stream size represented local habitat conditions). My assessment of abiotic characteristics suggested disturbed tributaries entering stable mainstems could have a strong influence on mainstem habitat characteristics downstream, however stable tributaries in

disturbed river systems had little impact on downstream habitat characteristics. This suggests that mainstem fish communities downstream of stable-disturbed confluence configurations are more likely to be influenced by the presence of the tributary than disturbed-stable configurations. This is quite obvious in my results. I observed similar fish abundance and community evenness scores in upstream mainstem and downstream branches in disturbed-stable configurations, whereas stable-disturbed configurations had much higher fish abundance and evenness scores in downstream branches compared to the mainstem upstream. Thus the principal mechanism structuring fish communities was not an inherent increase in local habitat heterogeneity downstream of confluences, as previously suggested (Rice, Greenwood & Joyce, 2001; Benda *et al.*, 2004), but instead the spatial arrangement of different habitat characteristics around the confluences drove changes in fish communities. That is, confluence configuration, rather than tributary presence per se, was most important. Often the influences of heterogeneity composition and configuration are not considered separately because they can be highly correlated in some systems (Bosem Baillod *et al.*, 2017). However, my findings indicate the specific combination of different habitat types within a landscape can be important, and can have considerable influence on biotic communities.

The presence of tributaries with different flow disturbance regimes to the mainstem river elevated fish community abundance and evenness, partially supporting my third and fourth hypotheses. However fish abundances were higher in disturbed tributaries with stable mainstems than in disturbed tributaries with disturbed mainstems. In comparison, stable tributaries juxtaposed with disturbed mainstems had lower abundances than tributaries in stable-stable configurations. This highlights the context-dependent spatial patterns in fish communities around confluences and shows the underappreciated role of spatially transferred influence through connected river networks. The potential for abiotic influences in freshwater systems to be transferred upstream to other branches through mobile biotic communities has

been understudied, but may play a very important role in structuring fish communities in heterogeneous riverscapes through trade-offs between resource availability and competitive and predatory interactions (e.g. Brewitt, Danner & Moore, 2017) . Spatial context is therefore critical to consider when evaluating transfer of influence through mobile populations across diverse, connected landscapes.

Configurations such as stable-disturbed and disturbed-stable confluences may create opportunities for source–sink and recolonisation dynamics by enhancing spatial heterogeneity in the riverscape (Pulliam, 1988; Woodford & McIntosh, 2010), and explain configuration-specific differences in branch-related patterns in fish abundance and evenness. Because the strength of biotic interactions is often related to variation in abiotic conditions (Power, Stewart & Matthews, 1988), the disturbed tributary in the stable-disturbed configurations may be changing the downstream flow disturbance regime sufficiently to moderate interspecific interactions and thus facilitate higher community evenness. In stable-disturbed configurations, both upstream mainstem and tributary evenness scores were low, but evenness was much higher in the mainstem downstream. Interestingly, the same was not true for disturbed-stable configurations. This suggests that the influence of the tributary on the physical characteristics downstream could be playing a role in addition to the presence of potentially more diverse source populations from different habitat types upstream, such as increasing downstream flow disturbance and moderating interspecific interaction strength. Salmoniids and galaxiids made up 98.6% of total fish abundance in this study, and trout in New Zealand are known to prey on, and competitively exclude, galaxiids (McDowall, 2003; McIntosh *et al.*, 2010). Thus it is possible that patterns in fish community evenness were driven by the relative abundance of galaxiids and trout, and the interactions between them.

Due to transferred influence upstream and downstream through mobile organisms, the spatial organisation of disturbance in a network has important implications for fish abundance and community evenness, particularly because the network propagates its effects in river ecosystems. While disturbance is widely regarded as a major driver of ecosystem structure, it is typically measured in terms of severity of impact (effect on local populations), intensity or magnitude, type (flood, fire, etc), temporal pattern (pulse, press or ramp), reoccurrence interval, and species vulnerability (Lake, 2000; Iwasaki & Noda, 2018). I suggest the addition of configuration of disturbance within a landscape could lend insight to studies of mobile organisms in heterogeneous environments where populations exist within a spatial mosaic of disturbance, and source–sink and recolonisation dynamics are likely to be operating.

Previously, ecologically 'significant' confluences have been thought to either be related to their spatial position in the network, or to their confluence symmetry ratio, i.e., the relative size of the tributary river compared to the mainstem (Kiffney *et al.*, 2006; Milesi & Melo, 2014; Jones & Schmidt, 2017). I found the spatial layout of abiotic conditions around confluences can play an important role in determining fish community composition by influencing the presence and configuration of spatial heterogeneity. Situations such as the stable-disturbed configuration, where tributary fish abundance was exceptionally high, illustrate the importance of taking the configuration of abiotic conditions around confluences into account when examining ecological patterns in river networks. An enduring problem in ecological conservation efforts is understanding the drivers behind complex spatial patterns across landscapes (Kennedy *et al.*, 2016). In streams this is further complicated by the dendritic network arrangement of the riverscape. Tributaries can clearly be an important source of large-scale heterogeneity in river networks (Kiffney *et al.*, 2006), supporting both higher fish densities and fish community evenness. To minimise the potentially dramatic outcomes of homogenization of freshwater environments (e.g. loss of flow disturbance from dams and flow regulation), conservation plans

need to address the spatial context of potential conservation sites and prioritize the protection of ecologically-important tributaries and their role in creating biologically significant confluences.

In the face of increasing homogenisation of ecosystems globally, developing and using methods to identify heterogeneity 'hotspots' for management and conservation is going to be useful. A legacy of viewing stream networks as homogenous segments connected at nodes, recently compounded by increasing use of GIS lines and nodes to represent riverscapes, has caused scientists to avoid sampling near confluences as they are perceived as being not representative of the segment as a whole due to confluence-related patterns (Jones & Schmidt, 2017). However, I contend that this method of sampling misses ecologically-important confluence dynamics that are capable of producing abundance hotspots and higher fish community evenness at large spatial scales. For example, disturbed tributaries in stable-disturbed configurations had significantly higher fish abundances than other configurations, and may therefore be a 'hotspot' of ecological significance for targeted conservation. Understanding the configurations of spatial heterogeneity that create biologically important 'hotspots' would enable conservation programs to target sites for restoration or protection to enhance particular threatened species abundances, maximise species diversity, or to mediate interspecific interactions between threatened native species and economically significant introduced species. By focussing on empirical research of dynamics at the intersections between different habitat types in heterogeneous landscapes, we may gain much more insight into spatial processes affecting metacommunities than by large-scale spatial models based on interpolations between infrequent data points.

Plate 2.Photographs of a stable spring-fed stream (left) and a disturbed braided river (right) typical of those in the Canterbury High Country.

Photos: Brandon Goeller (left) and Nixie Boddy (right)

Chapter Three:

Invasion across river networks: spatial configuration of heterogeneity affects the influence of invaders on native fish

Introduction

With landscape-scale habitat homogenisation making freshwater ecosystems among the most highly threatened in the world (Dudgeon *et al.*, 2006; Zeni & Casatti, 2014), coinciding with the impacts of invasive species being disproportionately severe compared to terrestrial environments (Moorhouse & Macdonald, 2014), it is pertinent to understand how environmental heterogeneity affects native–invasive species interactions in freshwater systems. Habitat heterogeneity can sometimes promote coexistence between strongly interacting native and invasive species (Cantrell, Cosner & Lou, 2007), whereas strong native–invasive interspecific interactions in homogenous environments can often lead to extirpation of native species (Maciel & Lutscher, 2018), so it is important to understand the characteristics of heterogeneity that facilitate coexistence. Moreover, understanding how native–invasive species interactions differ depending on the spatial configuration heterogeneity will progress our understanding of invasion in heterogeneous landscapes.

Conceptualizing river systems as spatially continuous habitat mosaics will be important for addressing the influence of heterogeneity on river communities (Fausch *et al.*, 2002). Discontinuities, potentially creating hotspots of heterogeneity, in river networks are most common at tributary confluences (Kiffney *et al.*, 2006). By joining streams with potentially different size, flow regimes, and water quality, confluences can be important sources of

environmental heterogeneity in river networks (Rice, Greenwood & Joyce, 2001; Benda *et al.*, 2004; Kiffney *et al.*, 2006). Furthermore, edge effects associated with confluence heterogeneity could be critical interfaces where biotic and abiotic processes interact to produce strong gradients in community composition (Fernandes, Podos & Lundberg, 2004; Czeglédi *et al.*, 2015; Chapter Two). The complexity of confluence geomorphology means determining relationships between tributary properties and aquatic communities is a major challenge (Rice, 2017). Nevertheless, a primary form of environmental variability in river systems is the frequency and severity of flow-driven physical disturbance (Lake, 2000), so I expected the configuration of flow disturbance around confluences would be a major factor determining the influence of a confluence on the structure of biotic assemblages.

In environments with spatially heterogeneous disturbance regimes, both biotic and abiotic factors are likely to structure communities (Jackson, Peres-Neto & Olden, 2001). In particular, heterogeneity in flow disturbance around confluences could influence the spatial distribution of non-native species, and therefore the outcome of native–invasive species interactions. Spatial heterogeneity in flow disturbance, for example, could control coexistence between native and invasive species with differing flow-related adaptations (Maciel & Lutscher, 2018).

The juxtaposition of contrasting flow-disturbance regimes between tributary, and upstream and downstream mainstem river branches means mobile taxa, like fish, can access habitats with contrasting physical characteristics (Rice, 2017). This enables individuals to move between habitat patches to complement or supplement resources, and provides connection between ‘source’ and ‘sink’ habitats (Fausch *et al.*, 2002). If predation pressure from invasive fish is patchy across a heterogeneous invaded riverscape, native fish could be limited by source–sink dynamics (Basse & McLennan, 2003; Woodford & McIntosh, 2010). Moreover, mobile species could propagate confluence heterogeneity effects, such as source–sink processes,

upstream and downstream from the confluence, and directional flow may mean influences are more easily propagated downstream than upstream. Therefore, spatial transitions in fish assemblage composition, from assemblages near the confluence influenced by confluence effects, to those further away potentially driven by local habitat conditions, are likely to occur more abruptly when travelling upstream from a confluence than downstream. Overall, if native–invasive interactions are moderated by flow disturbance, spatial patterns in the relative abundance of native and invasive species in invaded confluence habitats could be determined by the configuration of disturbance, and the direction and distance from a confluence. Thus, configuration of flow disturbance around confluences could explain much context-dependence in impacts of influential invasive predators.

The influence of confluence-related heterogeneity on interactions involving non-native Salmonidae is likely to be particularly important. Salmonids are one of the most widespread invasive groups in the world due to a long history of introductions to establish recreational fisheries, and their consequent effects on native fish has become a major concern (Fausch, 1988; Lowe *et al.*, 2000; Hasegawa, Mori & Yamazaki, 2016; Morita, 2018). For example, widely established populations of invasive trout have had severe effects on threatened native galaxiid species in the Southern Hemisphere (McDowall, 2006; Habit *et al.*, 2010; McIntosh *et al.*, 2010; Jones & Closs, 2015; Sowersby, Thompson & Wong, 2015). Importantly, the strong interactions of non-native salmonids play out across highly spatially heterogeneous river networks, and salmonids have both strong habitat preferences and are strongly influenced by physical habitat conditions like flooding (Fausch *et al.*, 2001; Budy *et al.*, 2008; Jellyman *et al.*, 2017). Large trout (e.g. > 150 mm fork length), in particular, exert strong predation pressure on galaxiids in New Zealand (McIntosh *et al.*, 2010), and occur in high densities in streams with stable flow, but are often less numerous in streams disturbed by flooding (Woodford & McIntosh, 2011). Therefore, strong trout predation in stable streams could lead to trout-

dominated assemblages, whereas native fish might persist in disturbed streams because of weaker interactions with trout. I therefore expected confluences with different configurations of flow disturbance to provide insights into the context-dependency driving the strength of native–invasive interactions in heterogeneous river networks.

To test a series of hypotheses evaluating if flow disturbance moderated native–invasive species interactions in river confluence habitats, I first established patterns of fish assemblage structure associated with 'stable' and 'disturbed' streams. I hypothesised that non-native salmonids would dominate stable streams and native galaxiids would form greater proportions of assemblages in flood-disturbed streams (H1). Secondly, I expected that the relative abundance of galaxiids would vary with confluence branch (upstream mainstem, tributary or downstream mainstem), confluence configuration (spatial arrangement of stable and/or disturbed flow conditions around the confluence) and distance from the confluence (H2). Here, I expected stronger distance-to-confluence patterns around confluences between stable and disturbed streams, than at confluences between two similar streams. I also hypothesised that distance-to-confluence effects would be stronger upstream, compared to downstream, due to flow directionality (H3). Finally, I predicted that the relative abundance of trout and galaxiids would be driven by large predatory trout reducing the abundance of small galaxiids (H4), with the strength of these interactions driven by the spatial configuration of flow disturbance around confluences (H5).

Methods

Field survey

I surveyed twelve river confluences in the Canterbury high country, South Island, New Zealand. Four confluence configuration categories were selected to include different combinations of flow-driven physical disturbance. These confluence configurations included:

(a) confluences between two ‘stable’ streams, (b) confluences between a ‘stable’ upstream mainstem and a ‘disturbed’ tributary, (c) confluences with a ‘disturbed’ upstream mainstem and a ‘stable’ tributary, and finally (d) confluences between two streams with ‘disturbed’ flow regimes (Fig. 2.1). Confluences were therefore labelled according to their configuration of flow-driven physical disturbance (Fig. 2.1). Where possible, I sampled confluences between third order streams (mainstems) and second order streams (tributaries) to control for the effects of stream size.

Each confluence survey involved sampling three ‘branches’ (Fig. 2.1). To ensure I sampled at an appropriate scale to resolve the spatial patterns of mobile species, I sampled five ‘reaches’ in each branch, making a total of 15 sampling reaches per confluence (Fig. 2.1). The length of each sampled reach was five times the stream width, and the distance between reaches was five times the average reach length for that branch. The reach sampled nearest the confluence began one reach length from the confluence, so the distance sampled for each branch was 130 times the stream width from the confluence. Sampling reach length was a constant multiple of the stream width, averaged over all five reaches in a branch, to avoid incorporating variability due to sampling different proportions of the available habitat depending on stream size (Peterson & Ver Hoef, 2010). Moreover, five stream widths was chosen to adequately represent the habitat complexity in the smaller streams, and not so large that it was unachievable to sample reaches in larger rivers (>10 m wide) in a day. Each sampling reach was single-pass electrofished in an upstream direction with push-nets, but without stopnets that spanned the river width at each end of the reach. Results of this approach correlate well with more intensive quantitative techniques in these streams, both for Galaxiidae (R^2=0.99) and trout (R^2=0.82) abundance (Chapter Two). Fish caught were identified to species and size classes recorded based on fork length. Galaxiidae were sorted into three size classes: young of year (< 60 mm), 1+ (60-90 mm), and 2+ (> 90 mm; Woodford & McIntosh, 2013). Salmonidae were also sorted

into three size classes: young of year (< 50 mm; Baltz & Moyle, 1984), medium (50-150 mm) and large (> 150 mm). The 150-mm size threshold was chosen to distinguish large brown and rainbow trout capable of consuming all sizes of galaxiids from medium size trout that are not capable of such predation (McIntosh, 2000).

To quantify flow disturbance in confluence branches, I used the Pfankuch River Disturbance Index (RDI), which combines visual estimates of 15 aspects of channel morphology, including indicators from both the stream bed and banks, to evaluate physical stability of a stream channel (Pfankuch, 1975; McHugh *et al.,* 2010; Jellyman *et al.,* 2013). RDI scores were used to classify upstream mainstem and tributary branches into 'stable' (RDI score < 100, low flow disturbance e.g. spring-fed streams) or 'disturbed' (RDI score > 100, high flow disturbance e.g. braided rivers). I used RDI scores above or below 100 to broadly categorise stream habitat types (Chapter Two). Confluences were labelled according to their upstream mainstem and tributary RDI scores, for example a confluence with a stable mainstem and a disturbed tributary was categorised as 'stable-disturbed.'

Statistical analysis

To evaluate fish assemblage change in response to different confluence configurations, I analysed the proportion of the fish assemblage that was composed of native species. This was calculated as the abundance of all native species in a reach as a proportion of the total fish abundance in the reach. Reaches with no fish present were removed from analyses.

Generalised linear mixed-effects models, created using the lme4 package in R (Bates *et al.,* 2015), were used to test for a three-way interaction between confluence configuration category (i.e., stable-stable, disturbed-disturbed, stable-disturbed or disturbed-stable), branch (i.e., tributary, upstream or downstream mainstem), and distance to confluence affecting the proportion of the fish assemblage that was native. The distance to confluence variable was

trialled in two forms. Firstly, linear distance in metres from the confluence to the nearest end of the reach, a method that represented travel distance between reaches. Secondly, I used distance measured in reach lengths from the confluence, a method incorporating differences in stream size which assumes fish assemblage patterns shift more gradually in larger rivers than small streams. A generalised linear mixed-effects model (glmer) was created with each option and ANOVA used to compare between models. There was no significant difference in variance explained, however the distance in metres model had a higher AIC score (815.3 vs. 802.2), and issues with model convergence and overdispersion. I therefore progressed with modelling using distance measured in reach lengths from the confluence.

ANOVAs were used to compare between models with and without interaction terms to determine their significance. These models were specified with binomial error distributions, and confluence configuration, branch and distance to confluence were included as fixed effects, and confluence identity as a random effect. Marginal and conditional coefficients of determination (Nakagawa & Schielzeth, 2013) were used to assess model fit, and were calculated using the MumIn package (Barton, 2016). R^2 marginal (R^2m) was used to express absolute model fit including only the fixed effects, while R^2conditional (R^2c) was used to express model fit including both fixed and random effects. Because confluence identity was a random effect in my model (i.e., which of the twelve confluences the reach in question was from), comparing the R^2m and R^2c values allowed the importance of confluence-specific effects in explaining variability in the data to be evaluated. Partial effects plots of the glmer model results were produced using the ggplot2 (Wickham, 2009) and effects (Fox, 2003) packages. All analysis was conducted in R 3.4.3 (R Development Core Team, 2016).

Results

Site and habitat characteristics

Using RDI scores to split upstream mainstem and tributary branches into 'stable' (RDI < 100) or 'disturbed' (RDI > 100), I was able to characterise the combinations of physical streambed disturbance in different confluence configurations. Mainstem RDI scores in disturbed-disturbed and stable-stable configurations changed little between upstream and downstream reaches, but the configurations with both stable and disturbed conditions upstream saw substantial changes in RDI scores downstream because of tributary influence (Table 3.1). As a result of tributary influence, mainstem reaches of stable-disturbed systems became much more disturbed (i.e., higher RDI score) downstream of the tributary confluence whereas disturbed-stable mainstems became more stable (i.e., lower RDI score) downstream (Table 3.1). A similar pattern of tributary influence was seen in the average daily temperature measures (Table 3.1). While average discharge was similar between disturbed mainstems (1.38 m^3/s) and stable mainstems (1.47 m^3/s), disturbed mainstems were generally much wider and shallower, reflecting a major difference in channel characteristics. This geomorphology difference could influence fish assemblage composition in addition to flow disturbance history.

Fish assemblage characteristics

In total, 4,368 fish from seven different species were caught. This included five native species: alpine galaxias (*Galaxias paucispondylus*), Canterbury galaxias (*Galaxias vulgaris*), kōaro (*Galaxias brevipinnis*), longfin eels (*Anguilla dieffenbachii*) and upland bullies (*Gobiomorphus breviceps*); and two non-native salmonids: brown trout (*Salmo trutta*) and

rainbow trout (*Oncorhynchus mykiss*). Average fish density per unit area was the lowest in disturbed-disturbed confluence configurations (0.1-0.19 fish / m^2) and highest in

Table 3.1: Biotic and abiotic characteristics of stream reaches, summarised by branch and configuration. Variables included average fish abundance (per metre squared of reach area), abundance range (maximum abundance– minimum abundance across all reaches), average Shannon Diversity Index value, maximum species diversity across all reaches, average proportion of total fish abundance at a site composed of native species, average substrate size (in mm, based on the Wolman Walk method), average stream width (m), average Pfankuch River Disturbance Index (RDI) score, and average daily temperature (ºC, based on average values calculated from hourly temperature measurements for the duration of the 2014 – 15 austral summer).

		Biotic					Abiotic			
Confluence configuration	Branch	Average fish abundance	Abundance range	Average Shannon Index	Maximum species diversity	Average proportion native	Average substrate size	Average stream width	Average RDI score	Average daily temperature
Disturbed-Disturbed	Upstream	0.1	0-0.77	0.28	4	0.32	129	7.2	139.3	11.1
	Tributary	0.19	0-0.91	0.11	3	0.64	99	5	146	11.3
	Downstream	0.1	0.01-0.32	0.53	4	0.46	90	9.8	138.1	10.7
Disturbed-Stable	Upstream	0.81	0-8.25	0.53	4	0.74	75	6.3	140.3	11.8
	Tributary	0.31	0-1.11	0.32	4	0.28	61	2.2	53.6	12.2
	Downstream	0.52	0.01-1.79	0.54	3	0.74	67	5.6	131.3	12.3
Stable-Disturbed	Upstream	0.38	0-1.2	0.24	2	0.18	80	3.1	54.8	8.6
	Tributary	1.33	0-3.6	0.29	3	0.89	83	2	119.2	10.8
	Downstream	0.82	0.14-1.8	0.66	2	0.59	77	3.6	77	9.7
Stable-Stable	Upstream	0.67	0-4.71	0.25	3	0.16	53	3.2	56.4	9.3
	Tributary	0.72	0-3.01	0.22	3	0.08	61	1.6	53.1	8.7
	Downstream	0.45	0.01-1.41	0.24	3	0.04	55	4.4	58.1	9.2

stable-disturbed confluence configurations (0.38-1.33 fish / m^2; Table 3.1). Species richness varied among sites and reaches from one to four taxa. Across sites, the most abundant taxa were *G. paucispondylus* (37.1% of total catch), *S. trutta* (28.4%), *O. mykiss* (18.7%) and *G. vulgaris* (13.1%), and the rarest taxa were *G. breviceps* (1.4%), *G.brevipinnis* (1.3%) and *A. dieffenbachii* (<0.1%). Trout and galaxiids combined made up 98.6% of total fish abundance on average in a reach, so any patterns in relative abundance of native fish reflect variation in abundance of these two groups. Average proportion of the fish assemblage that was native across all sites was 44%, ranging from 89% in stable-disturbed tributary branches to 4% in stable-stable downstream mainstem branches. Below, I focus on the drivers of the relative abundance of native galaxiids in these assemblages.

Relative abundance of native and introduced fish

Stable branches had significantly lower proportions of native fish in the community than disturbed branches, irrespective of confluence configuration ($\chi^2 = 37.15$, df = 1, $p < 0.001$; Fig. 3.1) in my glmer models including all sites (structured: proportion native ~ branch disturbance + branch + distance to confluence + (1|confluenceID)). Overall, non-native trout dominated the fish assemblage in stable branches throughout stream networks (low % native), and galaxiids made up the majority of the fish assemblage in disturbed branches (high % native), supporting my first hypothesis. Thus, higher densities of brown and rainbow trout were associated with more stable flow conditions.

My second hypothesis, that the proportion of the fish assemblage that was native would vary as a result of a three-way interaction between branch (i.e., flow direction matters), configuration (i.e., spatial context matters) and distance (i.e., proximity to confluence matters), was also supported ($\chi^2 = 50.7$, df = 11, $p < 0.001$, $R^2m = 0.36$, $R^2c = 0.66$). To better understand the mechanisms behind this three-way interaction, I analysed branches (upstream,

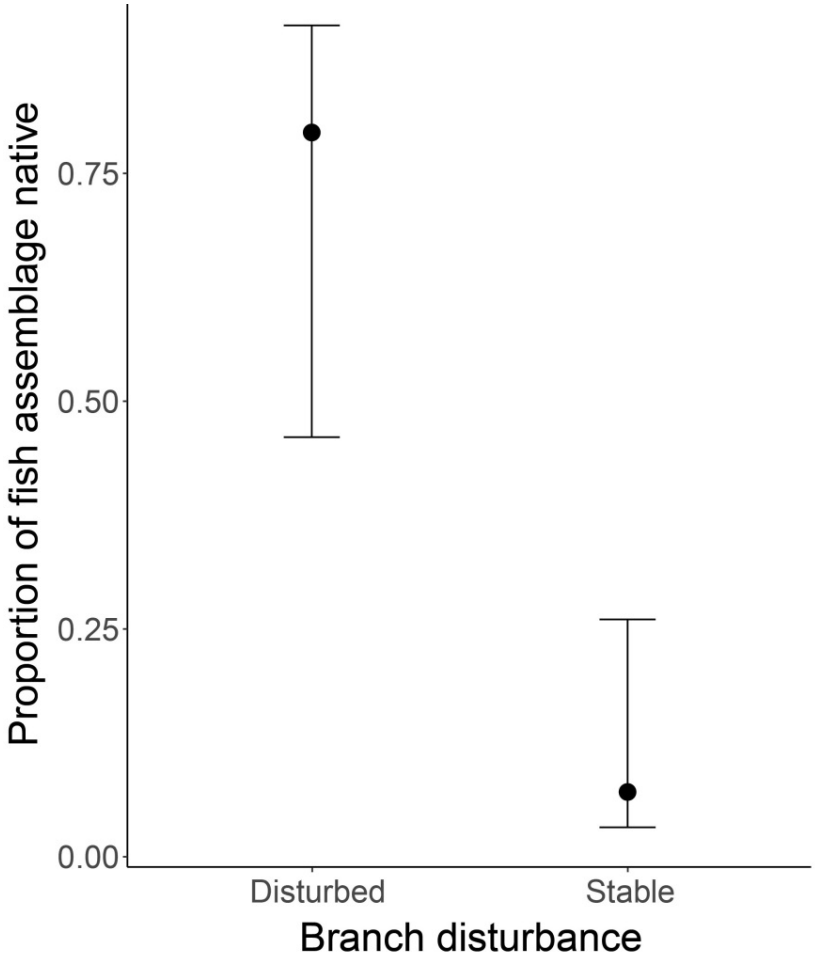

Fig. 3.1: Partial effects plot showing the proportion of the fish assemblage that was native compared to non-native, depending on whether the branch a site was located in was stable or disturbed. Points are model estimates with 95% confidence intervals.

tributary and downstream) separately to investigate the configuration by distance interaction in more detail.

For tributary branches, there was no significant interaction between confluence configuration and distance from confluence affecting the proportion of the fish assemblage that was native. Therefore, the distance to confluence effects were independent of changes in fish assemblages associated with confluence configurations. Preliminary graphing indicated branch disturbance may have more influence on proportion native than confluence configuration in tributary

branches, so I compared a model with 'configuration + distance' to a model with 'branch disturbance + distance.' 'Stable' branches had RDI scores less than 100, whereas 'disturbed' branches had RDI scores greater than 100. There was no significant difference in the variance explained by the two models (χ^2 = 2.19, df = 2, p =0.33); however, the branch disturbance model had a lower AIC score (181.1 vs. 183), so branch disturbance was a slightly better predictor. The model with branch disturbance as a factor showed that a significantly higher proportion of the fish assemblage was native in disturbed tributaries than stable tributaries (χ^2 = 5.7, df = 1, p = 0.017, R^2m = 0.28, R^2c = 0.71; Fig. 3.2). Distance to confluence was also a significant main effect in the tributary branch disturbance model, with higher proportions of native fish close to the confluence than further upstream (χ^2 = 4.93, df = 1, p = 0.026).

There was also a significant interaction between confluence configuration and distance to confluence, both in upstream (χ^2 = 8.56, df = 3, p < 0.036, R^2m = 0.4, R^2c = 0.77) and downstream (χ^2 = 17.53, df = 11, p < 0.001, R^2m = 0.42, R^2c = 0.74) mainstem branches (Fig. 3.3). For example, downstream reaches had very different proportions native compared to upstream reaches in stable-disturbed configurations, but little difference was observed in disturbed-stable configurations despite both configurations having the same pairs of branch disturbance upstream. Finally, disturbed-disturbed configurations had extremely low fish abundances, both upstream and downstream, and so the proportions of native fish were highly variable. Thus my prediction that there would be stronger distance to confluence patterns in configurations with a stable and a disturbed stream than in configurations with two similarly disturbed streams was only partially supported (Fig. 3.3).

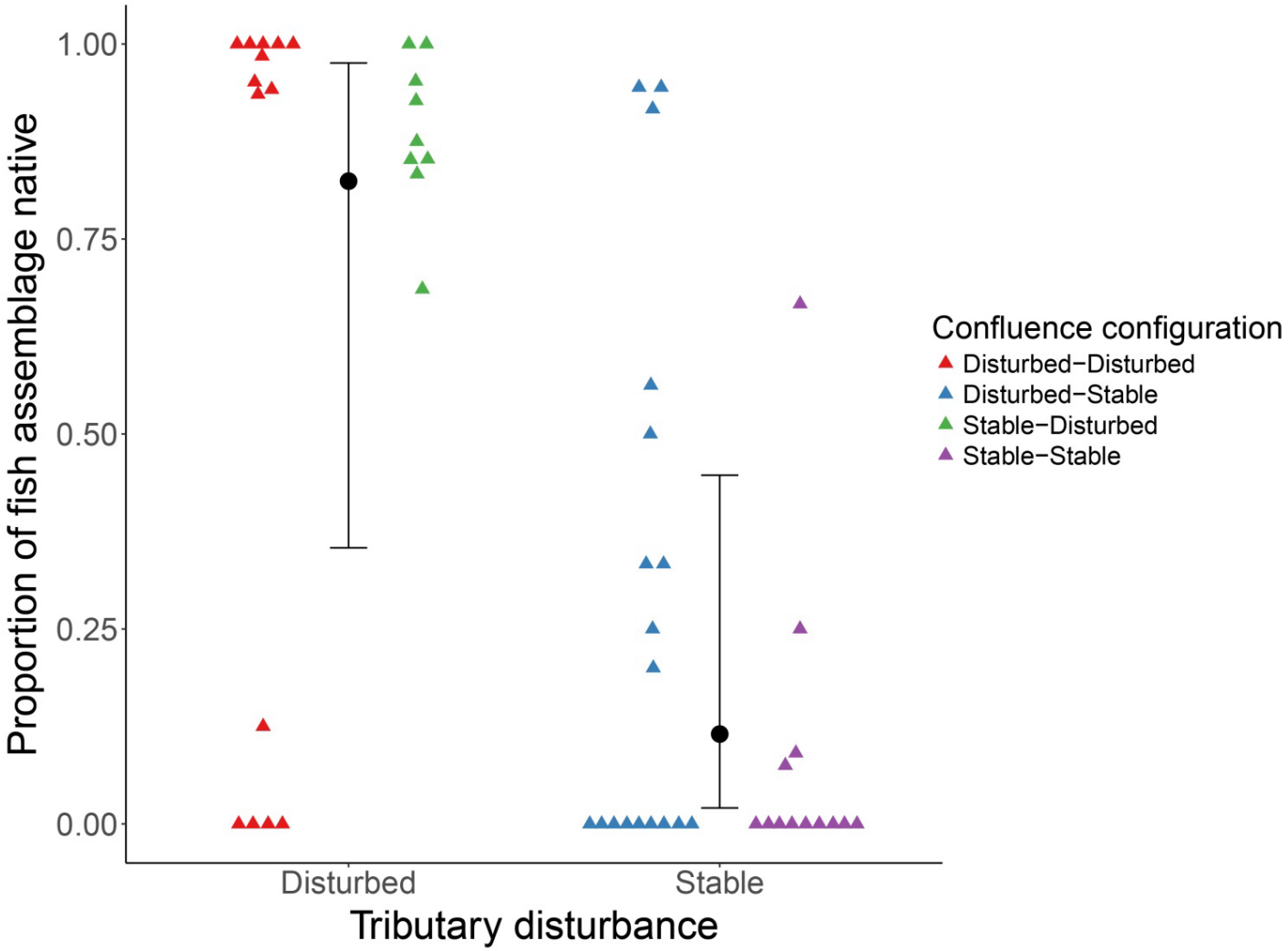

Fig 3.2: Partial effects plot showing difference in proportion of the fish assemblage that was native in tributaries depending on whether it was stable or disturbed. Circles are model estimates with 95% confidence intervals, and triangles are raw data points, coloured by confluence configuration (red, disturbed-disturbed; blue, disturbed-stable; green, stable-disturbed; and purple, stable-stable).

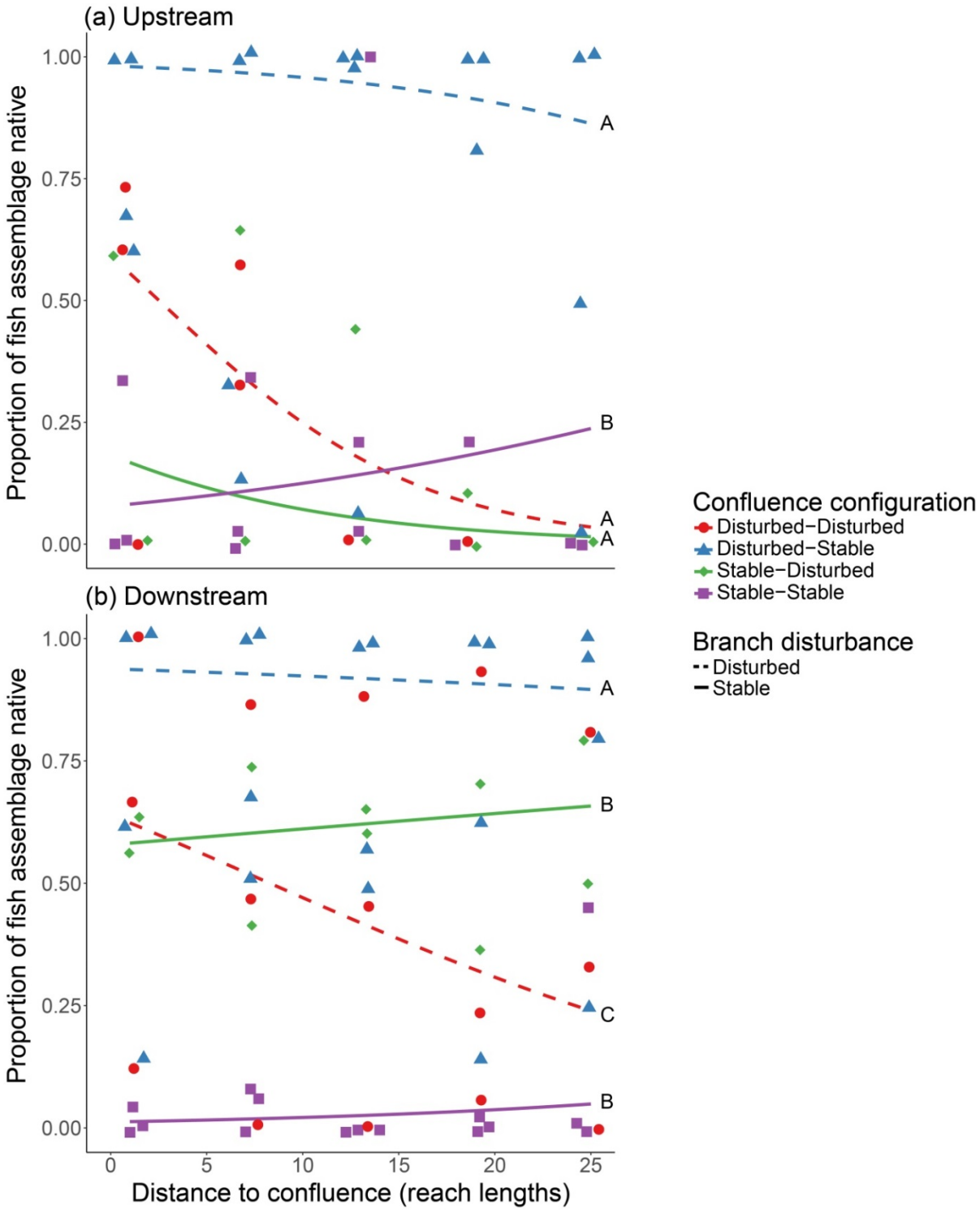

Fig 3.3: Partial effects plot showing interactions between confluence configuration and distance to confluence on the proportion of the fish assemblage that was native in both upstream (a) and downstream (b) reaches. Lines represent model estimates (solid, stable; and dashed, disturbed), and shapes and colours represent confluence configuration categories (red, disturbed-disturbed; blue, disturbed-stable; green,

stable-disturbed; and purple, stable-stable). Lines with significantly different slopes are coded with different letters (A-C).

In upstream mainstem branches, the native portion of the fish assemblage declined with increasing distance from the confluence in disturbed-disturbed, disturbed-stable and stable-stable configurations (Fig. 3.3a). However in stable-stable upstream mainstem branches the proportion native increased further from the confluence (Fig. 3.3a). Overall, regardless of distance to confluence, mainstem reaches upstream of confluences tended to have lower relative abundance of native fish in stable branches than disturbed branches, as I expected, but distance from confluence effects differed depending on confluence configuration.

In mainstem branches downstream of confluences, disturbed-stable and disturbed-disturbed confluence configurations both had higher relative abundance of native fish near the confluence than further from it (Fig. 3.3b). Both configurations also had significantly different relationships between relative abundance of native fish and distance to confluence compared to all other configurations, with proportion native decreasing much more strongly with distance to confluence in disturbed-disturbed than disturbed-stable configurations (Fig. 3.3b). Stable-disturbed and stable-stable configurations did not have significantly different relationships, with proportions native increasing with distance from the confluence in both configurations (Fig. 3.3b). Thus my third hypothesis that distance to confluence effects would be stronger upstream compared to downstream due to directional flow was supported, with steeper slopes between relative abundance of native fish and distance from the confluence in upstream mainstem than in downstream mainstem branches (Fig. 3.3).

Size class analysis

To examine mechanistic drivers of changes in the proportions of fish that were native, I first tested disturbance effects in tributary branches, the simplest of the branch-related patterns, and

examined the relative abundance of vulnerable galaxiid size classes. Proportional abundance of each galaxiid size class differed significantly with disturbance in tributaries ($\chi^2 = 56.3$, df = 2, $p < 0.001$; Fig. 3.4a). Young-of-year galaxiids made up a significantly larger proportion of total fish abundance in disturbed tributaries, increasing the relative abundance of native fish in disturbed compared to stable tributaries (Fig. 3.4a). Disturbed tributaries also contained significantly higher proportions of 1+ galaxiids compared to stable tributaries, but they still made up a relatively small proportion of total fish abundance (Fig. 3.4a). No significant difference was detected in the relative abundance of 2+ galaxiids in stable and disturbed tributary branches. Trout sizes also differed significantly with tributary disturbance ($\chi^2 = 16.7$, df = 2, $p < 0.001$; Fig. 3.4b), with disturbed tributaries having significantly lower proportions of large trout (i.e., > 150 mm), likely limiting the strong predatory influence of trout in those areas (Fig. 3.4b).

The relationship between the configuration of flow disturbance and changes in the proportion of fish that were native were more complex in mainstems upstream and downstream of confluence branches due to the influence of distance from confluence. For example, higher relative abundances of native fish in upstream mainstem branches near the confluence in disturbed-disturbed, disturbed-stable and stable-disturbed configurations were driven by high abundances of YOY galaxiids, which were associated with extremely low abundances of trout > 150 mm at these locations. In disturbed-disturbed and stable-disturbed reaches the abundance of YOY galaxiids was dramatically reduced moving upstream from the confluence, coinciding with higher relative abundances of trout (Fig. 3.3).

To further investigate the potential effects of large trout on YOY galaxiid abundance I analysed their abundance across all configurations and branches: relative abundance of YOY galaxiids significantly decreased with increasing proportions of large trout ($\chi^2 = 100.3$, df = 1, $p < 0.001$,

$R^2m = 0.22$, $R^2c = 0.62$; Fig. 3.5). This model predicted < 0.01% of the fish present at a site would be composed of YOY galaxiids if large trout (> 150 mm) made up

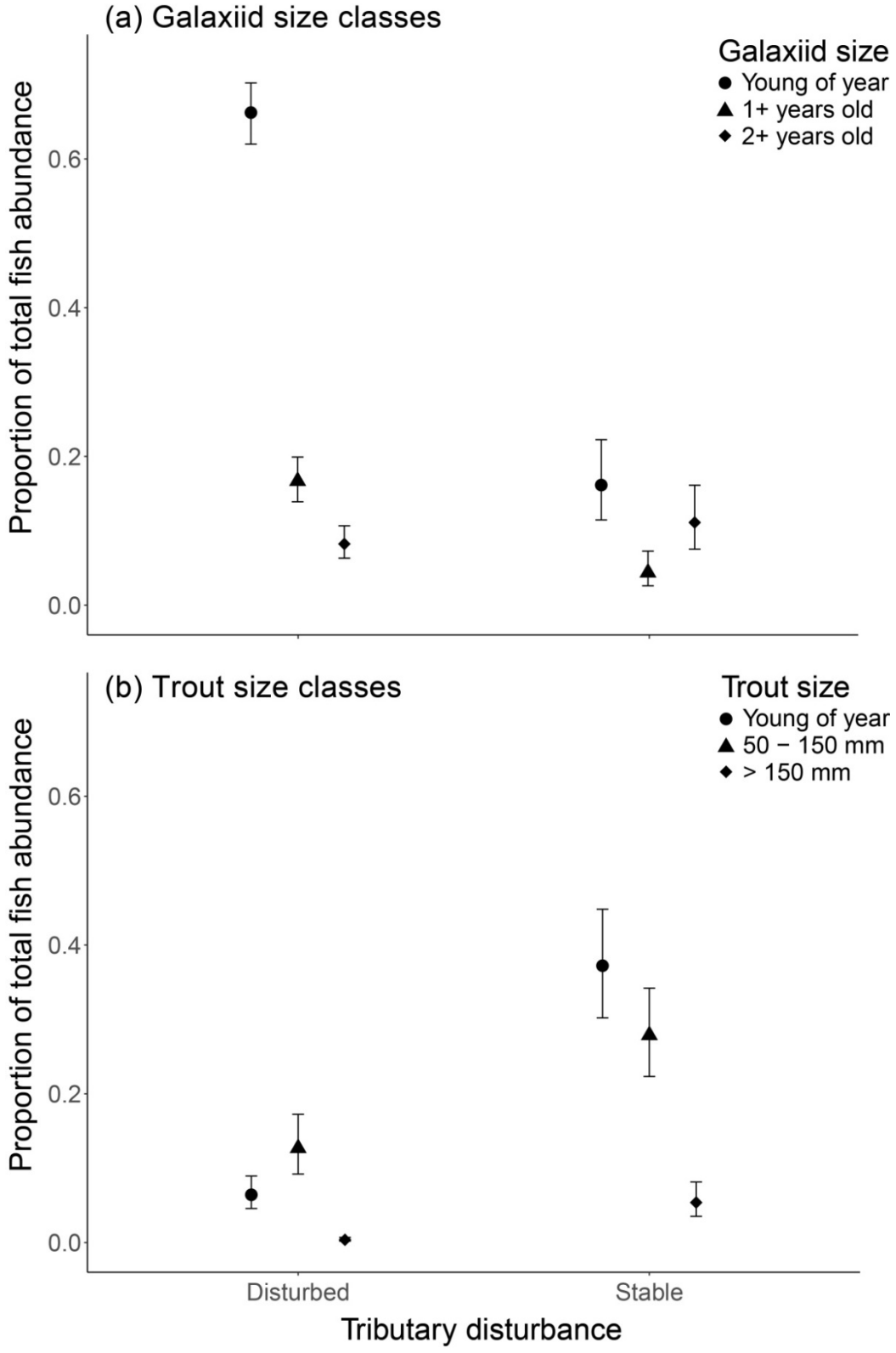

Fig 3.4: Partial effects plot showing proportions of total fish abundance made up by each size class of galaxiid (a) and trout (b) in tributaries depending on whether the tributary was stable or flood-disturbed. Points are model estimates with 95% confidence intervals. Shapes represent different fish size classes.

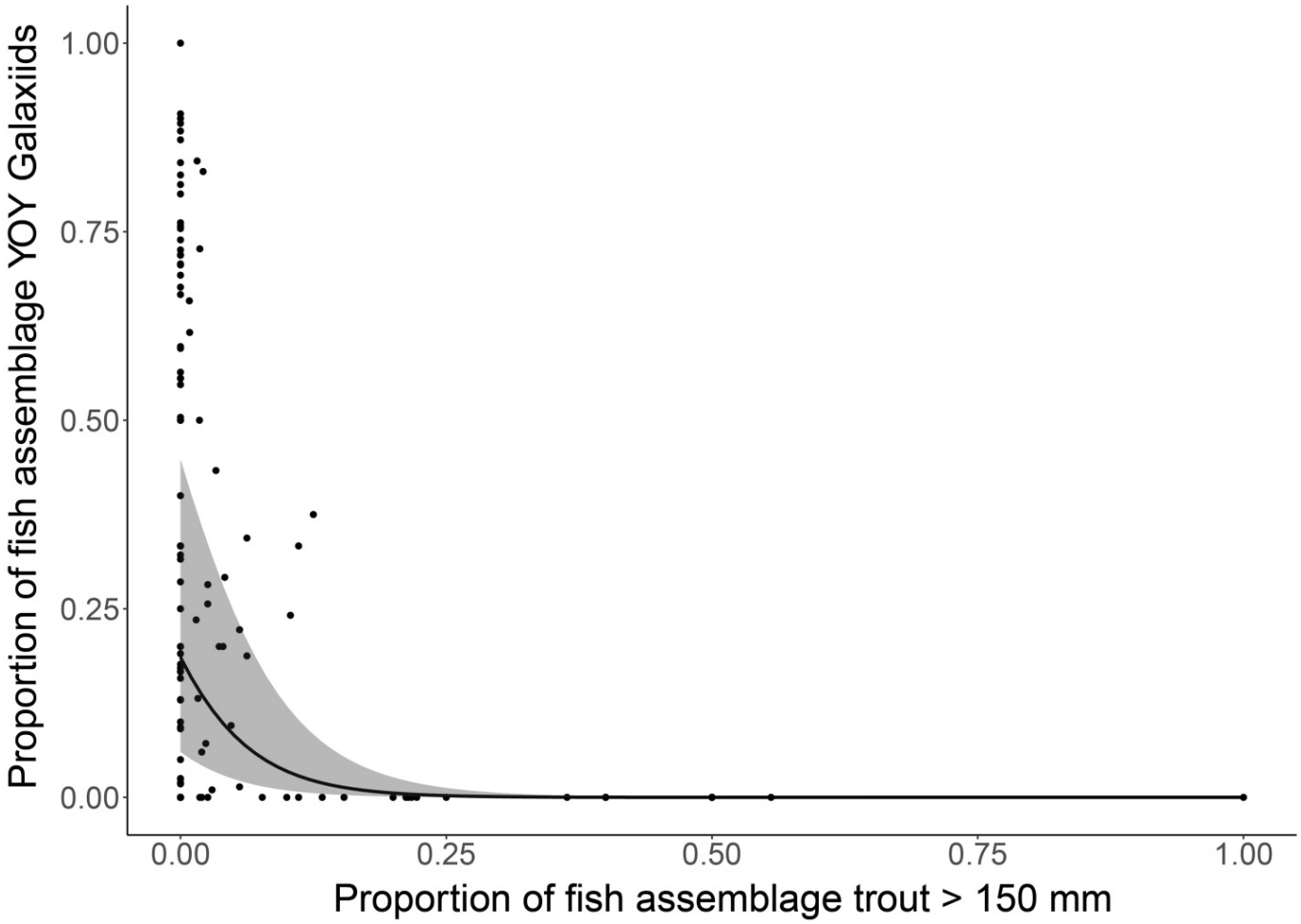

Fig 3.5: Partial effects plot showing the proportion of the fish assemblage comprised of young of year (YOY) galaxiids in relation to the proportion of the fish assemblage that was made up of trout larger than 150 mm long. Points represent raw data values, the line is the model estimate and the shaded area is the 95% confidence interval.

greater than 16% of the assemblage. These results support my fourth hypothesis, that galaxiid abundance would be driven by large predatory trout. Importantly, my results reveal that this pattern was primarily driven by the vulnerability of YOY galaxiids to large trout. This was a fairly simple relationship in the tributary branches, but patterns were made more complex by distance to confluence effects, and tributary disturbance regimes modifying downstream habitat conditions in upstream mainstem and downstream branches. These results support my fifth hypothesis that the outcome of interspecific interactions was contingent on the spatial configuration of disturbance within branches.

Discussion

As human activities continue to fragment and homogenise habitats, it is important to understand the role of spatial heterogeneity in invasion processes (Olden, 2006; Maciel & Lutscher, 2018). Despite the importance of confluences as sources of heterogeneity in river systems, little is known about how the spatial configuration of habitat around confluences influences interactions between native and non-native species in invaded riverscapes (Cathcart *et al.*, 2018). I examined how different configurations of flow disturbance around confluences influenced spatial patterns in the distribution of native galaxiids and introduced trout in New Zealand rivers. My results revealed highly context-dependent distributions of native galaxiids and non-native trout, which depended on confluence configuration, distance to confluence and direction of flow. These factors created distinct patterns in relative abundance of fish driven by the configuration of disturbance around confluences.

Many of the patterns I found in native and non-native species relative abundance were ultimately driven by the sensitivity of non-native trout to flood disturbance. I found both brown and rainbow trout densities and distributions were negatively affected by flood-disturbance, as shown in previous studies in New Zealand (Jowett & Richardson, 1989; Jowett, 1990). As a

result, the proportion of the fish assemblage that was native differed depending on flood disturbance, with low proportions of native species in stable branches, and high proportions of native fish in more disturbed branches, supporting my first hypothesis. This pattern was driven by high abundances of young-of-year (YOY) galaxiids in more disturbed branches, and very little co-occurrence between YOY galaxiids and large trout in more stable stream branches where large trout were more numerous, supporting my fourth hypothesis. Strong predation pressure on non-migratory galaxiids by large trout is a common feature of trout-galaxiid interactions, and is especially evident given the rarity of galaxiid fry in trout-invaded reaches (Jellyman & McIntosh, 2010; Woodford & McIntosh, 2010). Therefore, predation by large trout on YOY galaxiids was likely a primary driver of native fish distributions across all stream branches and confluence configurations. Invasive species abundance often drives their impact on native species (Kumschick *et al.*, 2015; Latzka *et al.*, 2016), so by limiting densities of large piscivorous trout, flood disturbance likely mediates the strength of native–invasive interactions in these riverscapes.

Confluences are likely to considerably alter fish assemblages across riverscapes by causing spatial heterogeneity in disturbance regimes which in turn mediates these interactions between native and non-native species. Changes in fish abundance and assemblage composition around confluences in South Island high country rivers are driven by the spatial configuration of flow disturbance at the confluence (Chapter Two). Together, these results indicate that patterns in fish assemblages are likely driven by interspecific interactions acting out over a complex spatial habitat mosaic. I found a significant interaction between the configuration of flow disturbance, spatial position with regard to the confluence (tributary, upstream mainstem or downstream branch) and distance to the confluence affecting the proportion of fish assemblages composed of native species, supporting my second hypothesis. The interaction between confluence configuration and distance to confluence suggests spatial processes such as dispersal and

recolonisation may be occurring in these systems, and influencing the relative abundance of native and invasive fish.

Assemblages in systems with high environmental variability are predicted to be driven more by stochastic processes such as recolonisation dynamics and presence of refugia, compared to those with low variability, where convergent processes like biological interactions might be stronger (Schlosser & Kallemeyn, 2000; Chase *et al.*, 2009). However, to further develop our understanding, we need to appreciate how these processes combine at network nodes such as confluences. I found that connection of stable-flowing and highly flood-disturbed streams by a confluence interacted to create important spatial patterns in species assemblages because of the strong invader-driven interactions in stable habitats. For example, in stable-disturbed confluence configurations, stable upstream mainstems contained very low proportions of native fish (< 20% of the fish assemblage native), the disturbed tributaries had very high proportions of native fish (> 80%), but downstream, there was higher co-occurrence, with fish assemblages around 60% native. This spatial pattern was likely driven by trout-dominated assemblages in the stable upstream mainstem and flood-adapted galaxiid-dominated fish assemblages in the disturbed tributary, both providing source populations to downstream reaches. Invasive trout and non-migratory galaxiids co-occur much more often than they coexist (Woodford & McIntosh, 2010), and it is unknown whether these downstream reaches are sink habitats for native fish. Thus, while I can establish that heterogeneity in flood disturbance between upstream mainstem and tributary branches can increase co-occurrence between native and invasive fish species downstream of the confluence, I do not know if this heterogeneity actually facilitates coexistence such that galaxiids can successfully reproduce in these locations.

The influence of tributaries on the physical characteristics downstream of confluences could also play a role in determining whether co-occurrence occurs in addition to the presence of potential source populations upstream. The stable-disturbed (i.e., disturbed tributary) confluence configuration mentioned above contrasts with the patterns found in the disturbed-stable (i.e., stable tributary) confluences, which had almost entirely native fish assemblages in the mainstem both upstream and downstream of the confluence despite the presence of a stable tributary with very low proportions of native fish. Because the strength of biotic interactions is likely driven by abiotic conditions, the disturbed tributary in the stable-disturbed configurations changing the downstream flow to more intermediate levels of disturbance may have been sufficient to moderate interspecific interactions between galaxiids and trout, and thus promote co-occurrence by limiting predation by large trout downstream. This is consistent with previous studies reporting native species persistence in invaded habitat being mediated by disturbance limiting predation pressure, and fish diversity being maximized at intermediately disturbed sites (Jackson, Peres-Neto & Olden, 2001; Woodford & McIntosh, 2011). Therefore heterogeneous disturbance conditions around confluences could facilitate co-occurrence, but not necessarily coexistence, between native and invasive fish species through colonist supply or by moderating interaction strength.

Another important aspect of these confluence influences is that species interactions could also limit the direction and distance that individuals can disperse (Ganio, Torgersen & Gresswell, 2005). I found a significant interaction between confluence configuration and distance to confluence in both mainstem upstream and downstream branches that affected the relative abundance of native fish. Thus, it was not simply the presence of heterogeneity, but also the spatial configuration and proximity of various habitats, that were important in determining assemblage composition. Significant distance-to-confluence effects affecting fish assemblages in branches, both upstream and downstream of the confluence, show that mobile species can

propagate confluence influences in both the upstream and downstream directions. Directional flow likely created effects that were more easily propagated downstream than upstream, thus transitions in the proportions of native fish observed occurred more abruptly upstream from a confluence than downstream. This supports my third hypothesis, and is consistent with upstream shifts in assemblages away from confluences being often abrupt (Thornbrugh & Gido, 2010). Nevertheless, some tributaries are capable of impacting mainstem biotic communities up to several kilometres downstream depending on the mainstem disturbance regime (Rice, Greenwood & Joyce, 2001; Benda *et al.*, 2004; Woodford & McIntosh, 2011). I was able to detect upstream shifts in the relative abundance of native fish, both in upstream mainstems and tributaries, however downstream effects were weak, so I was unable to resolve the downstream extent of confluence effects, or if interactions were affected indefinitely downstream.

The propagation of confluence effects was directionally-biased, suggesting source–sink dynamics likely will be too. Certain confluence configurations likely create opportunities for source–sink and recolonisation dynamics by enhancing riverscape spatial heterogeneity, which could explain some configuration-specific differences in distance-related patterns I observed. Elevated relative abundances of native fish near confluences in stable upstream branches of stable-disturbed configurations where large trout would normally eliminate galaxiids are likely indicative of sink populations of galaxiids. Galaxiids can persist in sink habitats near sources where propagule pressure is high, but because propagule pressure decreases with increasing distance to the source (Woodford & McIntosh, 2011), proximity to source populations likely affects spatial patterns in co-occurrence within sink habitats in invaded riverscapes. Dramatic shifts in community composition in close proximity to confluences have also been associated with fish moving between more physiologically suitable, but food-limited habitat, and less-suitable but more resource-rich stream branches (Brewitt, Danner & Moore, 2017). In the case

of vulnerable native species in invaded riverscapes, these 'attractive sink' habitats could represent resource-rich habitats offering higher growth rates but with a trade-off of increased mortality, and potentially reduced chances of successful reproduction (McIntosh *et al.*, 2010; Timus *et al.*, 2016). This could be problematic if species vulnerable to attractive sinks do not perceive any increased predation risk.

Stable-stable confluence configurations were characterised by universally low relative abundance of native galaxiids regardless of distance to confluence and were likely sink habitat resulting from strong interspecific interactions with trout (Woodford & McIntosh, 2010). In contrast, disturbed-disturbed configurations had extremely low total fish abundance, and highly variable proportions of native fish. These disturbed-disturbed situations are likely the result of disturbance-driven 'pseudosinks' rather than interactions between native and non-native species. For example, Woodford and McIntosh (2010) identified flood-disturbed and large streams as likely pseudosinks for non-migratory galaxiids in New Zealand, whereby very low abundances of galaxiids were isolated from source streams, and as such, susceptible to localised extinction. Therefore confluences with homogenous configurations of flow disturbance, whether stable or disturbed, tended to have lower abundance, and lower proportions of native fish. An interesting point for further development, therefore, would be to directly contrast fish abundance and proportion of the fish assemblage that is native in homogenous versus heterogeneous configurations of flow disturbance to determine the inherent value of confluence-related heterogeneity for fish assemblages.

In the face of increasing homogenisation of ecosystems globally, developing and using methods to identify heterogeneity influences for management and conservation is going to be crucial. My results, revealing the role of spatial configuration of flow disturbance around confluences in influencing the relative abundance of native and invasive fish species, in conjunction with

previous studies (Thornbrugh & Gido, 2010; Brewitt, Danner & Moore, 2017; Peláez, Azevedo & Pavanelli, 2017), highlight the importance of spatial context in determining local assemblage characteristics. Importantly, understanding how invasive species impacts vary with physical heterogeneity, provides an opportunity to strategically prioritize management efforts at large spatial scales to minimise invader impacts (Hansen *et al.*, 2013; Vander Zanden, Hansen & Latzka, 2017). Moreover, revealing the causes of context-dependence in invasive predator impacts, helps fill the knowledge gap around how species traits and spatial heterogeneity influence invader impacts (Kumschick *et al.*, 2015; Latzka *et al.*, 2016), potentially enabling targeted management of high risk locations. In addition, confluence-focussed management could promote co-occurrence, and hopefully coexistence, as an effective solution in globally common situations where invasive fish species such as trout are recreationally and economically important, but are impacting endangered native species. Management actions such as environmental flow setting or maintenance of existing heterogeneity could prioritize the protection or restoration of mutually beneficial configurations of flood disturbance in these scenarios (Chen & Olden, 2017).

Plate 3. Photographs of an adult Galaxias paucispondylus *(top) and large* Salmo trutta *(bottom) caught during fieldwork in the Canterbury High Country.*

Photos: Nixie Boddy (top) and Simon Litchwark (bottom)

Chapter Four:

Spatial heterogeneity in flow-disturbance influences abundance and temporal stability in native–invasive species co-occurrence in riverscapes

Introduction

Ecological systems are commonly influenced by spatial heterogeneity in environmental processes creating geographically-patchy habitats (Pickett & Cadenasso, 1995). In freshwater ecosystems, much like their terrestrial and marine counterparts, small-scale habitat heterogeneity is often associated with higher species richness and spatial variability in assemblage composition, such as amongst stream fishes (Fernandes, Podos & Lundberg, 2004; Smith & Mather, 2013; Peláez, Azevedo & Pavanelli, 2017). In contrast to the well-studied effects of small-scale environmental heterogeneity on communities, the relationship between larger scale environmental heterogeneity and ecosystem stability is not well understood. McCluney *et al.* (2014) hypothesised that a decrease in habitat heterogeneity in a river network will tend to amplify catchment-scale variation in ecological communities over time, suggesting homogenisation of abiotic variables could lead to destabilisation of communities through decreases in the resistance and resilience of freshwater biota to disturbance. Moreover, spatial dynamics such as dispersal between habitat patches can stabilise biotic communities and facilitate the coexistance of interacting species (Bellmore, Baxter & Connolly, 2015; Gravel, Massol & Leibold, 2016). Spatially heterogeneous disturbance in riverscapes could therefore

play a crucial role in dispersal-aided community stability by producing variation in source populations for recolonisation.

Disturbance is a key component of all ecosystems affecting biological communities at both large and small spatial and temporal scales (Fraterrigo & Rusak, 2008). Habitat heterogeneity can buffer the impacts of disturbance at a regional scale, by creating spatial variation in the magnitude, duration and frequency of disturbances (Donohue *et al.*, 2016). Thus, individuals from less-affected areas are able to recolonise more heavily impacted areas nearby to produce higher temporal stability in communities (Turner, 1989; Caswell & Cohen, 1991; Brown, 2007). While stability has many meanings in ecology (Grimm & Wissel, 1997), here it is defined as the mean of an ecosystem function, divided by its temporal standard deviation (Wilcox *et al.*, 2017). In freshwater ecosystems, large-scale habitat heterogeneity could be increased through the spatial juxtaposition of habitats with very different disturbance regimes (Kennedy *et al.*, 2016). Because fluctuations in stream flow are the major form of disturbance in stream ecosystems (Hart & Finelli, 1999; Bunn & Arthington, 2002; Poff & Zimmerman, 2010), we might expect variation in flood-disturbance regimes to be a primary source of large-scale heterogeneity in river systems, and a key factor determining stream fish assemblage composition and stability at these scales.

It has been accepted that abiotic factors such as environmental heterogeneity and disturbance history may play a significant role in community stability at broad spatial scales (Anderson, 2017; Wilcox *et al.*, 2017), however the strongest environmental control of species composition has been predicted at intermediate spatial scales, where dispersal is both not so high as to obscure the effects of spatial heterogeneity, or so low that differences in assemblage structure are more related to historical processes (Peláez, Azevedo & Pavanelli, 2017). Therefore, studies using different spatial scales may have resulted in the inconsistent reports of

the importance of interspecific interactions in structuring fish communities (Jackson, Peres-Neto & Olden, 2001). Variability in interspecific interactions and invasive species impacts has often been termed 'context dependent' (Chamberlain, Bronstein & Rudgers, 2014; Latzka *et al.*, 2016; Vander Zanden, Hansen & Latzka, 2017). In the case of native–invasive interactions, understanding the drivers behind these variable outcomes is crucial. Spatial heterogeneity may provide differentially-disturbed, spatially-juxtaposed source populations to sustain coexistence or co-occurrence of native and invasive species near habitat boundaries, thus playing a large role in promoting community stability at larger spatial scales (Wilcox *et al.*, 2017). In contrast, homogenization of environmental conditions or disturbance impacts could significantly reduce ecosystem stability by reducing both spatial variability in species interactions and population-specific responses to disturbance (Wilcox *et al.*, 2017). Therefore spatial heterogeneity in disturbance across a network may moderate the effects of negative interactions, such as those between native and invasive species, and promote more temporally stable coexistence between native and invasive species.

Although large-scale spatial heterogeneity is obviously important, ecologists have struggled to find simple techniques to investigate relationships between communities and spatial structure at large spatial scales, especially in rivers (Flitcroft *et al.*, 2012). While stream networks are inherently complex and highly variable, aquatic communities are likely structured by the fundamental processes of hydrology and topography (Campbell & McIntosh, 2017), therefore an initial step to understanding riverscape-scale biotic variability is identifying consistent patterns in river networks associated with these processes (Ganio, Torgersen & Gresswell, 2005). In river systems, confluences can be 'hotspots' of heterogeneity at large spatial scales, depending on the arrangement of habitat types, with ecological influences disproportionate to their small spatial extent (Czeglédi *et al.*, 2015; Cathcart *et al.*, 2018). Benda *et al.* (2004) found small-scale habitat heterogeneity increased downstream of confluences when very

different disturbance regimes were spatially juxtaposed, therefore we might expect large-scale heterogeneity in disturbance regimes within river networks to create spatially predictable patterns in biotic assemblages associated with that heterogeneity.

Although tributary-mainstem interactions are often described as complex, common properties of all river systems such as flow disturbance may provide an opportunity to identify crucial confluence characteristics and assess their impacts on aquatic assemblages. Because confluence heterogeneity, in the form of different configurations of flow disturbance regimes, influences stream fish abundance and assemblage composition (Chapters Two & Three), spatial heterogeneity in flow-disturbance regimes around confluences could influence ecosystem stability. In ecology, heterogeneity can refer to habitat diversity (the number of habitat types in an area), habitat complexity (the spatial arrangement of habitat patches), or temporal variability in within-habitat environmental conditions (Palmer, Menninger & Bernhardt, 2010). In addition, quantitative heterogeneity can be viewed as a gradient of variability and complexity from low to high, with low being homogeneity (Li & Reynolds, 1995). Here I use heterogeneity to describe habitat diversity of river confluences in a binomial manner, i.e., the tributary and mainstem branches of a confluence have either similar ('low' heterogeneity) or very different ('high' heterogeneity) flow disturbance regimes.

I evaluated if heterogeneity in flow disturbance conditions around confluences in the South Island high country of New Zealand influenced the density and relative abundance of native and invasive fish. I hypothesised that heterogeneous confluences would be associated with higher fish abundances per metre of stream length compared to more homogenous confluences (H1). I predicted this would be the result of interactions between native fish and introduced salmonids; trout can be strong competitors and predators in these river systems (McIntosh *et al.*, 2010; Woodford & McIntosh, 2013). I expected these interactions would be reflected in

the relative proportion of the fish community composed of native compared to invasive species. Secondly, I expected that more homogenous environments would contain less stable communities, indicated by higher temporal variation in the relative abundance of native and invasive fish species in homogenous confluences compared to heterogeneous confluences (H2).

Methods

Field survey

I surveyed eight river confluences in the Canterbury high country, New Zealand, over three time periods, autumn (March 2015), spring (November 2015) and summer (February 2016). Confluences were divided into two categories, 'high' and 'low' heterogeneity, based on the combination of upstream mainstem and tributary abiotic conditions associated with physical disturbance from flooding. To quantify flow disturbance in confluence branches I used the Pfankuch River Disturbance Index (RDI) which combines visual estimates of 15 aspects of channel morphology including indicators from both the stream bed and banks to evaluate physical stability of a river channel (Pfankuch, 1975; McHugh *et al.*, 2010; Jellyman *et al.*, 2013). These scores were used to classify upstream mainstem and tributary branches into 'stable' (RDI score < 100, low flow disturbance e.g. spring fed streams) or 'disturbed' (RDI score > 100, high flow disturbance e.g. braided rivers). In these systems, RDI scores above or below 100 can be used to broadly categorise stream habitat types, capturing variation associated with water temperature, substrate size and stream size, in addition to flood disturbance (Chapter Two).

'High heterogeneity' confluences included those with both 'stable' and 'disturbed' upstream branches, i.e., a confluence with a 'disturbed' upstream mainstem and a 'stable' tributary, or vice versa. The 'low heterogeneity' category consisted of either confluences between two

‘stable’ streams, or confluences between two streams with ‘disturbed’ flow regimes (Fig. 4.1a). Where possible, I sampled confluences between third order mainstems and second order tributaries to control for the effects of stream size.

Each confluence survey involved sampling six reaches, two in each of the three stream ‘branches’ (Fig. 4.1b). Sampling reach length was five times the stream width, and the distance between reaches was five times the average reach length for that branch. The reach sampled nearest the confluence began one reach length from the confluence, so the distance sampled for each branch was 40 times the stream width from the confluence. Sampling reach length was a constant multiple of the stream width, averaged over both reaches in a branch, to avoid incorporating variability due to sampling different proportions of the available habitat depending on stream size (Peterson & Ver Hoef, 2010). Moreover, effects of confluences on stream fish assemblages extend approximately two reaches upstream, so sampling two reaches in each direction from the confluence was sufficient to represent changes in fish assemblages associated with confluence-related heterogeneity (Chapter Three). Each sampling reach was single-pass electrofished in an upstream direction without stopnets; the results of this method correlate well with more intensive quantitative techniques in these systems, for both Galaxiidae (R^2=0.99) and Salmonidae (R^2=0.82) abundance (Chapter Two). Fish caught were identified to species, and size classes recorded based on fork length. Galaxiidae were sorted into three size classes: young of year (YOY, < 60 mm), one year old (1+, 60-90 mm) and two or more years old (2+, > 90 mm; Woodford & McIntosh, 2013). Salmonidae were also sorted into three size classes: YOY (< 50 mm; Baltz & Moyle, 1984), medium (50-150 mm) and large (> 150 mm). The 150-mm size threshold was chosen to

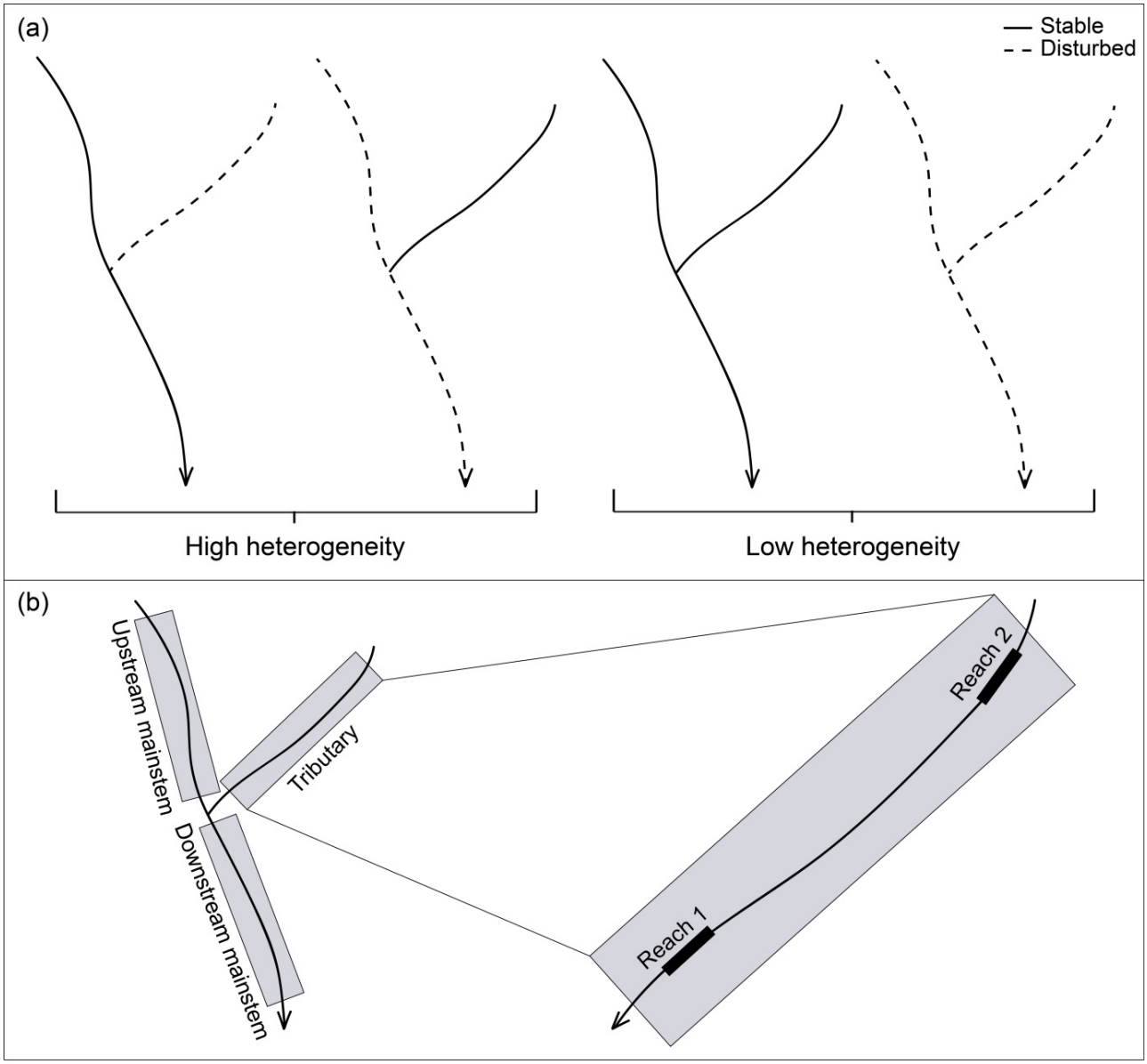

Fig. 4.1: Field sampling design showing conditions in 'high' compared to 'low' heterogeneity confluences (a), based on the combination of stable and disturbed flow regimes (solid and dashed lines, respectively) within the three 'branches' in each confluence (upstream mainstem, tributary and downstream mainstem, b). 'Stable' streams had low flood disturbance, and 'disturbed' streams had high flood disturbance. Within each branch, two reaches were sampled, making a total of six sampling reaches per confluence replicate.

distinguish large brown and rainbow trout because trout > 150 mm are capable of excluding all sizes of Galaxiidae from stream reaches through predation (McIntosh, 2000).

Statistical analysis

I evaluated the relationship between responses: fish abundance per metre of stream length and proportion of the fish assemblage that was native; and the predictor variable, confluence heterogeneity, using confluences as replicates. Abundance per metre of stream length was used as a measure of fish density because stream widths changed over time, which could inflate fish abundance per unit area estimates through habitat compression. Mean fish abundance per metre was calculated as the average of the six sampled reaches in each confluence, also averaged over time.

To evaluate fish assemblage change in response to confluence heterogeneity, either high or low, I analysed the proportion of the fish assemblage that was composed of native fish, trout, or galaxiids. This was calculated as the abundance of all native species (or all trout species, or all galaxiid species) in a reach as a proportion of the total fish abundance in the reach. Reaches with no fish present were removed from this analysis. The coefficient of variation (CV) in the proportion of the fish assemblage that was native, expressed as the percentage of the mean represented by the standard deviation, was used to analyse patterns over time. The CV calculated for each stream reach was averaged to give mean CV in proportion of the fish assemblage that was native for each confluence, whereby high CV in proportion of the fish assemblage that was native indicated large changes in the relative abundance of trout and galaxiids over time, and small CV values indicated stable ratios of trout and galaxiid abundance over time.

Generalised linear mixed-effects (glm) models, created using the lme4 package for R (Bates *et al.*, 2015), were used to test the effect of confluence heterogeneity (high or low) on the response variables. To evaluate confluence heterogeneity itself, I used the CV of the six RDI scores recorded for each confluence as a measure of physical variability in a glm. High CV in RDI

scores meant the confluence contained highly heterogeneous conditions (i.e., both stable and disturbed flow conditions), and low CV meaning conditions throughout the confluence were relatively similar, whether they be stable or disturbed, and thus heterogeneity was low.

Hypothesis One was tested using fish abundance models fitted with a Quasi-Poisson distribution in the 'glm' function, both to avoid the overdispersion present in standard Poisson models (Zeileis, Kleiber & Jackman, 2008), and because fish abundance per linear metre, the response variable, was not expressed in integers. To assess Hypothesis Two, examining the proportion of the fish assemblage that was native, 'glm' Quasi-Binomial models were used to overcome issues with overdispersion associated with using the Binomial family of models. Confluence heterogeneity in these models was included as the only fixed effect. The exception to this modelling format was the model for the proportional abundance of different trout and galaxiid size classes. This had proportion of total fish abundance in the confluence as a response variable, and unique confluence ID, plus an interaction between size class and confluence heterogeneity as fixed effects. ANOVAs were used to assess all model fits and evaluate significance with alpha set at 0.1 to overcome possible type-two statistical errors associated with the small sample sizes inherent in measuring temporal variability of populations. Plots of the glm model results were produced using the ggplot2 (Wickham, 2009) and effects (Fox, 2003) packages for R. All analysis was conducted in R 3.4.3 (R Development Core Team, 2016).

Results

Confluence heterogeneity and site characteristics

My sites encompassed a range of natural flood disturbance regimes, with RDI scores varying from 37 to 152, and reach lengths ranged from 6 to 40 m long. Temporal variation in stream width ranged from 0 to 7.4 m, with a median change over time of 0.5 m, justifying the choice of abundance per metre rather than per metre squared.

The coefficient of variation in RDI scores was significantly higher in 'high' heterogeneity confluences than 'low' heterogeneity ($F_{1,6}$ = 36.55, $p < 0.001$; Fig. 4.2), indicating my confluence heterogeneity categories reflected variability in flood-disturbance in these systems.

Fish assemblages

The 6380 fish caught included five native species: alpine galaxias (*Galaxias paucispondylus*), Canterbury galaxias (*Galaxias vulgaris*), kōaro (*Galaxias brevipinnis*), longfin eels (*Anguilla dieffenbachii*) and upland bullies (*Gobiomorphus breviceps*); and two non-native salmonids: brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*). Across sites and sampling times, the most abundant taxa were *G. paucispondylus* (47.1% of total catch) and *O. mykiss* (25.9%), followed by *S. trutta* (15.7%) and *G. vulgaris* (9.8%). The rarest taxa were *G. breviceps* (1.3%), *A. dieffenbachii* (0.2%) and *G.brevipinnis* (<0.1%). Trout and galaxiids combined made up 98.7% of total fish abundance, so patterns in fish abundance and proportion of the fish community that was native reflect variation in abundance of these two groups.

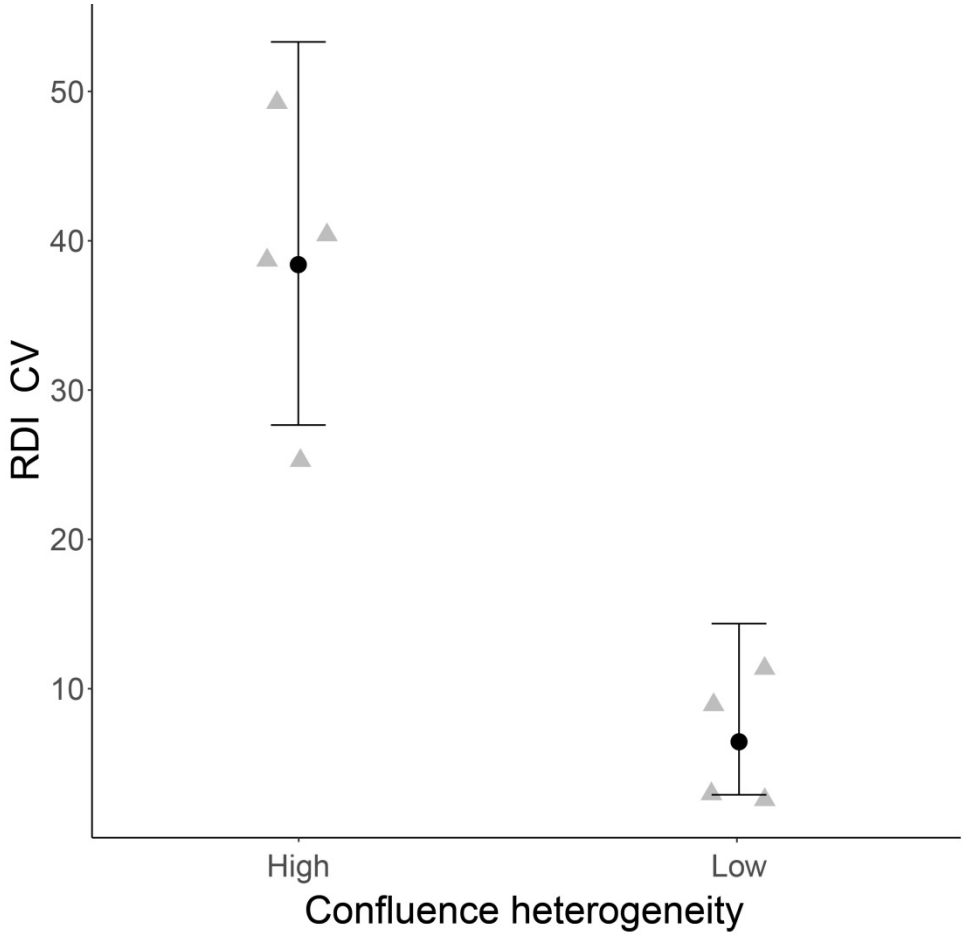

Fig. 4.2: Coefficient of variation (CV) in River Disturbance Index (RDI) scores measuring flood-related disturbance in relation to high or low confluence heterogeneity. Circles are model estimates with 95% confidence intervals, and triangles are raw data points.

Confluences with 'high' heterogeneity had significantly higher mean fish abundance per metre of stream length than 'low' heterogeneity confluences ($F_{1,6}$ = 5.34, p = 0.06; Fig 4.3b), supporting Hypothesis One, however abundance was relatively variable between confluences (Fig. 4.3a). Total fish abundance was not significantly affected by time ($F_{2,21}$ = 0.14, p = 0.87), or an interaction between time and confluence heterogeneity ($F_{2,12}$ = 2.21, p = 0.15), reflecting the lack of consistent temporal patterns in trout or galaxiid abundance per metre of stream reach (Fig. 4.4). Trout abundance per metre was highly variable, and was not associated with

confluence heterogeneity (Fig. 4.4b). Galaxiid abundance per metre of stream length, however, was significantly greater in high heterogeneity confluences than homogenous confluences ($F_{1,6}$ = 12.66, p = 0.012; Fig. 4.5). Therefore, the higher fish abundances in high heterogeneity confluences (Fig. 4.3) were driven by the abundance of galaxiids. Because patterns in total fish abundance per metre were driven by high abundances of native galaxiids, the proportion of the fish assemblage that was native was also likely to change in response to confluence heterogeneity.

Confluence heterogeneity did not significantly affect the mean proportion of the fish assemblage that was native ($F_{1,6}$ = 1.92, p = 0.22), but the mean proportion of the fish assemblage in different size classes of either trout (YOY, < 150 mm, > 150 mm) or galaxiids (YOY, 1+ and 2+ years old) differed significantly depending on confluence heterogeneity ($F_{5,30}$ = 3.76, p = 0.009). Generally a higher proportion of the fish assemblage at a confluence was composed of YOY and 1+ galaxiids in high heterogeneity confluences, compared to low heterogeneity (Fig. 4.6). In contrast, generally higher proportions of the fish assemblage were comprised of the trout size-classes in homogenous confluences (Fig. 4.6).

Finally, looking at temporal patterns in native–invasive species co-occurrence, the mean coefficient of variation in proportion of the fish assemblage that was native was significantly higher in low heterogeneity confluences than high heterogeneity confluences ($F_{1,6}$ = 7.26, p = 0.036; Fig. 4.7), supporting Hypothesis Two. Therefore the relative abundance of native and invasive fish was more stable over time in high heterogeneity confluences compared to homogenous confluences.

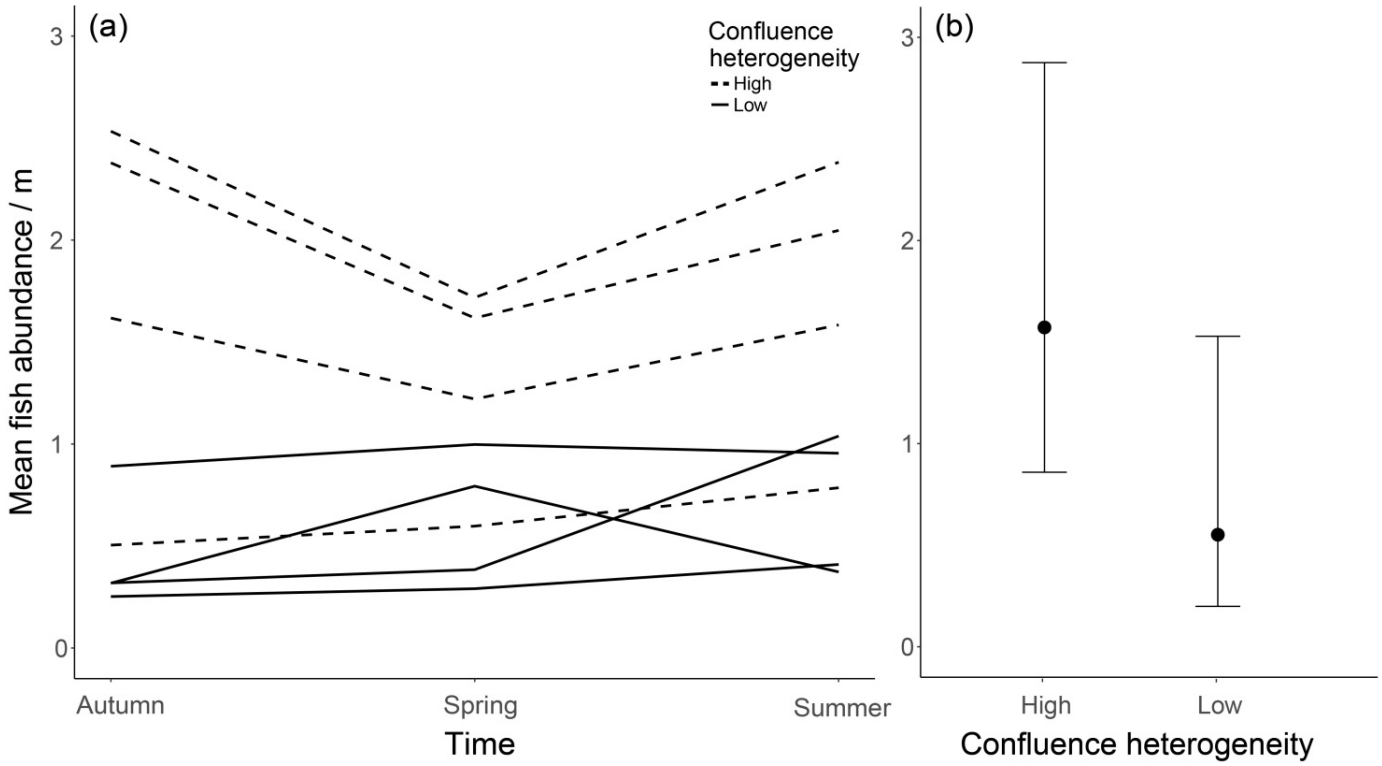

Fig. 4.3: Mean fish abundance per metre (averaged over the six reaches in each confluence) in relation to (a) the three measured time periods, autumn (March 2015), spring (November 2015) and summer (February 2016), and (b) high or low confluence heterogeneity (mean abundance averaged over six sampling reaches and three time periods). Lines represent each confluence in panel a (solid, low heterogeneity; and dashed, high heterogeneity). In panel b points are model estimates with 95% confidence intervals.

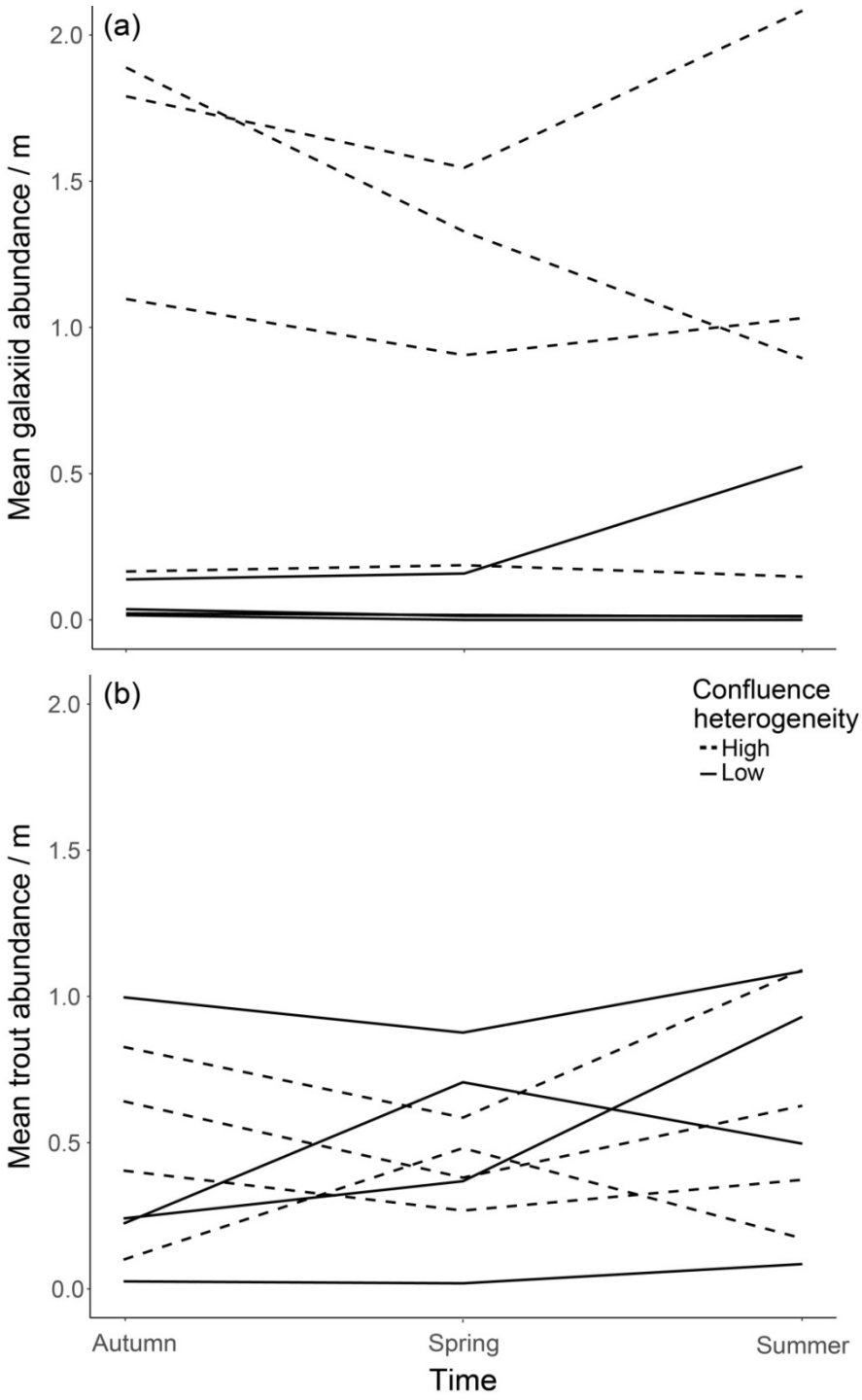

Fig. 4.4: Mean galaxiid (a) and trout (b) abundance per metre (averaged over the six reaches in each confluence) across the three measured time periods, autumn (March 2015), spring (November 2015) and summer (February 2016). Lines represent each confluence (solid, low heterogeneity; and dashed, high heterogeneity).

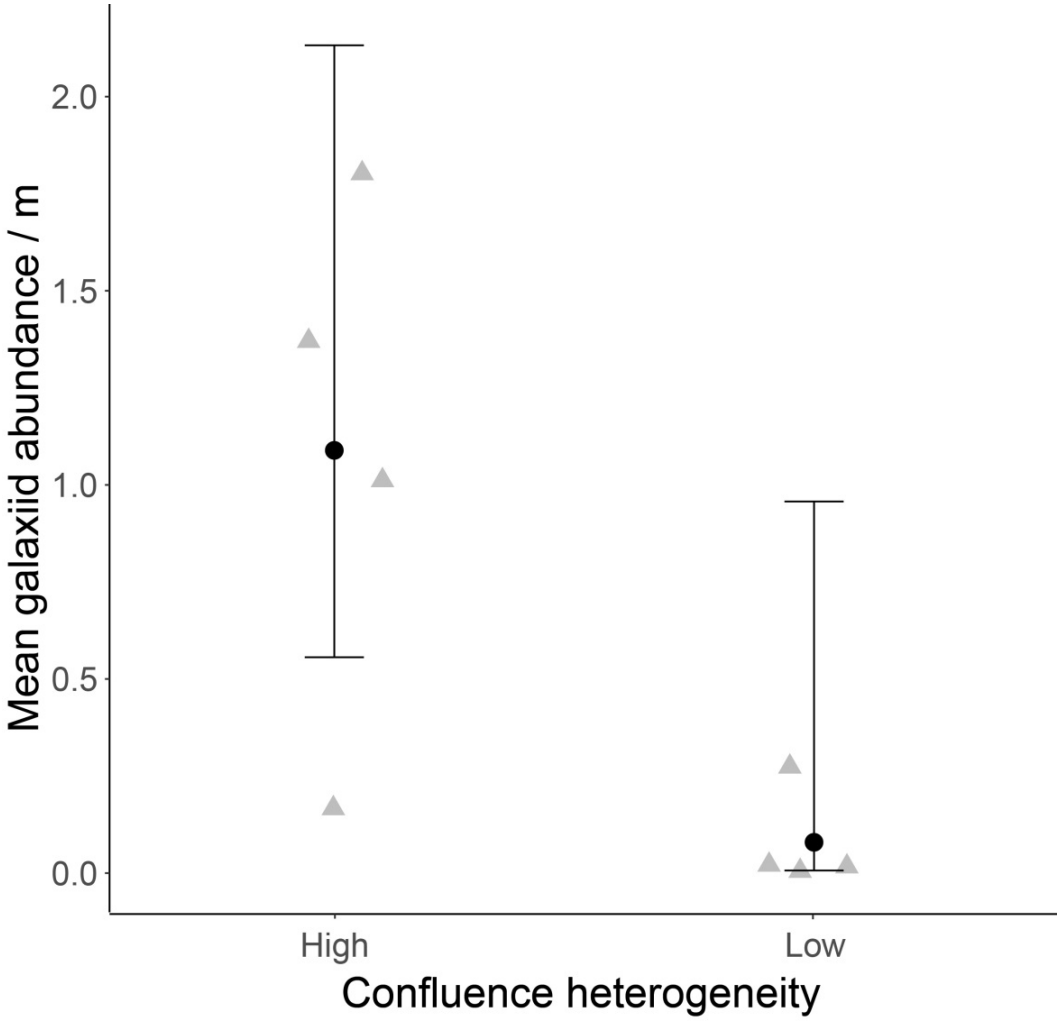

Fig. 4.5: Mean galaxiid abundance per metre, averaged over six sampling reaches and three time periods, in confluences with high or low heterogeneity. Circles are model estimates with 95% confidence intervals, and triangles are raw data points.

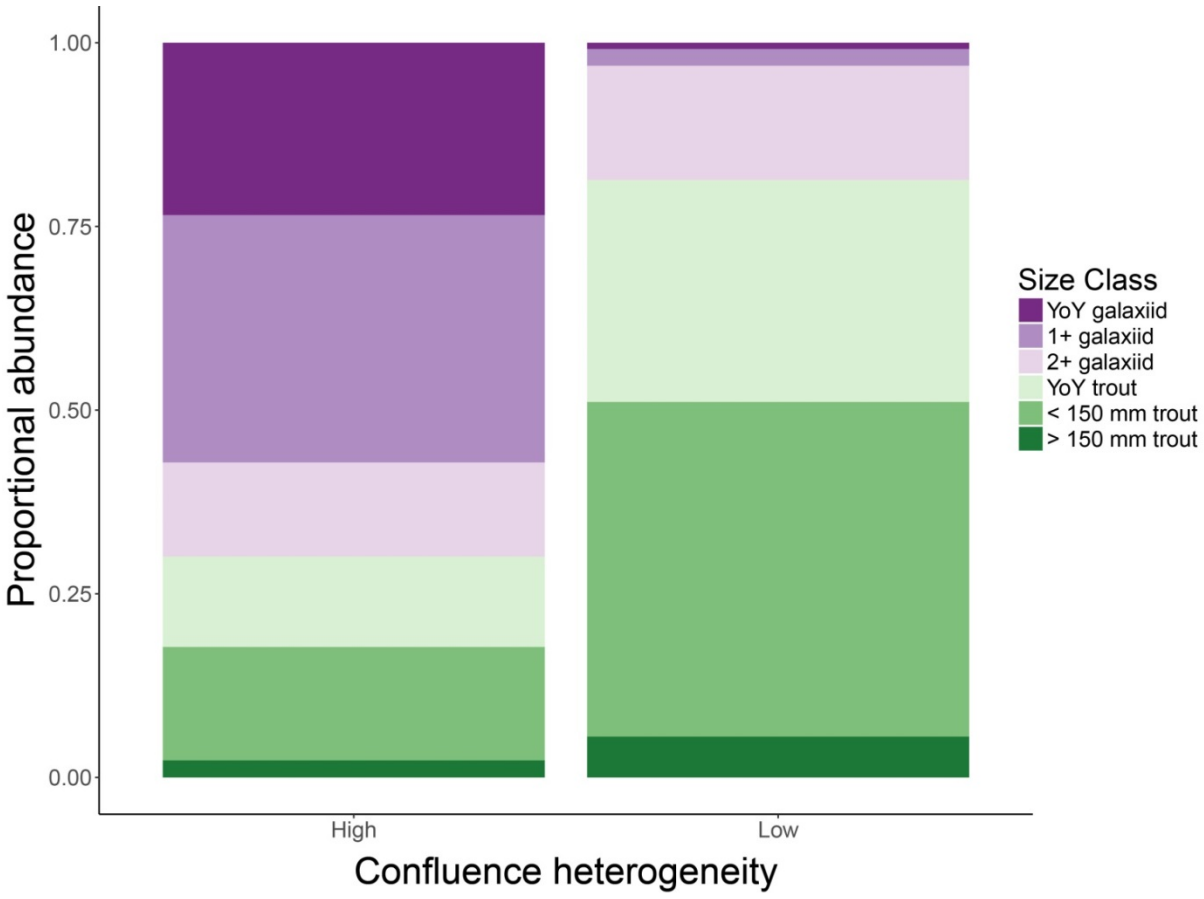

Fig. 4.6: Proportion of total fish abundance (summed across all reaches, times, and confluences within a heterogeneity category) consisting of each galaxiid and trout size class, depending on high or low confluence heterogeneity. Colours represent size classes of galaxiids (young of year, 1-2 years old and more than 2 years old) and trout (young of year, < 150 mm long and > 150 mm long).

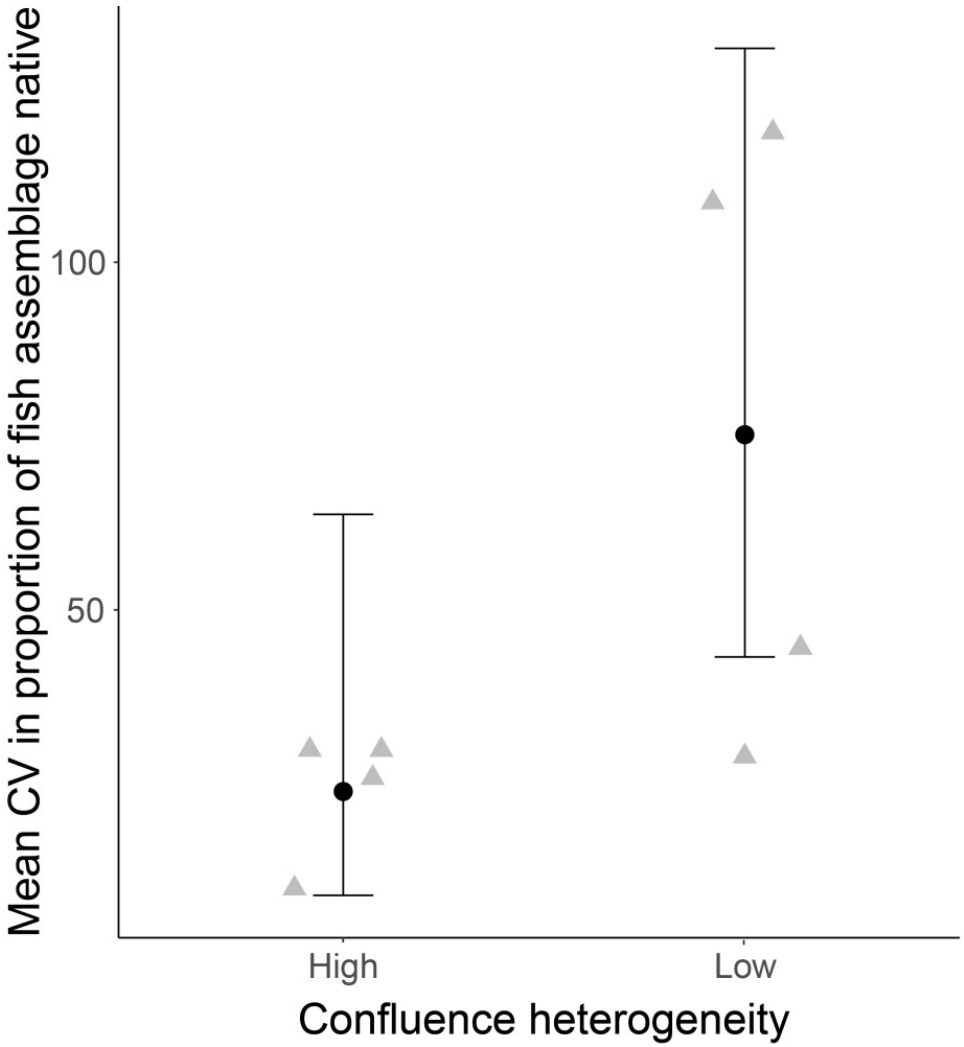

Fig. 4.7: Mean coefficient of variation (expressed as percentage of the mean represented by the standard deviation, averaged over time) in proportion of the fish assemblage that was native, depending on high or low confluence heterogeneity. Circles are model estimates with 95% confidence intervals, and triangles are raw data points.

Discussion

It is widely accepted in community ecology that environmental and biotic processes combine to produce spatial variability in community structure, through processes such as dispersal limitation and spatial connectivity (Grenouillet, Pont & Herisse, 2004; Leibold *et al.*, 2004; Heino *et al.*, 2015). Moreover, within a network, better connected communities are expected to receive more migrants, buffering them from demographic stochasticity and allowing fast recovery from disturbance events (Dala-Corte, Becker & Melo, 2017). McCluney *et al.* (2014) suggested habitat heterogeneity in a river network would be associated with lower catchment-scale temporal variation in communities through increased resilience to disturbance, compared to abiotically homogenous networks. Despite increasing focus on network structure and its influence on aquatic communities, empirical studies of the configuration of abiotic conditions around confluences and their influence on aquatic community dynamics are rare (Kiffney *et al.*, 2006). I examined how heterogeneity in flow disturbance around confluences influenced the abundance and structure of fish assemblages in New Zealand rivers. My results revealed that while fish assemblages around confluences are highly variable, heterogeneity in flow disturbance conditions around confluences created predictable patterns in fish abundance, and temporal stability in the relative abundance of native and invasive fish species in the river systems.

Confluence-effects on aquatic communities vary due to the ratio of tributary to mainstem size, basin shape and size, confluence density, configuration of conditions and geometry of streams in the network (Benda *et al*., 2004; Kiffney *et al*., 2006; Chapters Two & Three). However, the effects of the arrangement of abiotically different streams around a confluence, that is confluence heterogeneity, are poorly understood (Kiffney *et al.*, 2006; Rice, 2017). Given that numerous ecological processes potentially shaping communities operate at landscape scales,

the juxtaposition of contrasting flood-disturbance conditions may support higher densities of stream fish through processes such as habitat complementation, source–sink population dynamics, resource subsidies and dispersal connectivity (Fausch *et al.*, 2002; Kiffney *et al.*, 2006; Campbell Grant, Lowe & Fagan, 2007; Rice, 2017). I found heterogeneity in the flood-disturbance regimes between the two stream branches joining at a confluence was associated with higher mean fish abundance, supporting my first hypothesis. This aligns with previous research associating spatial complexity in hydrological variability with higher aquatic productivity, abundance and biomass (Chisholm, Lindo & Gonzalez, 2011; Garcia, Schnauder & Pusch, 2012).

Conversely, when flood-disturbance conditions in the two streams joining were similar, resulting in a homogeneous confluence, fish abundance was lower. Different processes likely drove lower total fish abundance, depending on disturbance regime. I expected assemblages in streams with low spatial environmental variability would be driven more by biological interactions, in contrast to those that were highly disturbed, which might be more affected by recolonisation dynamics and presence of refugia (Schlosser & Kallemeyn, 2000; Garcia, Schnauder & Pusch, 2012). Thus, strong interactions between native galaxiids and invasive trout likely led to low fish densities in homogenous confluences of stable streams, whereas around homogenous confluences of disturbed streams, the environmental harshness likely produced lower fish densities. Higher fish densities in heterogeneous confluences were driven by increases in galaxiid abundance, predominantly high numbers of young-of-year (Chapter Three). This increased survival or density of galaxiids was likely made possible by large predatory trout being less abundant in high heterogeneity confluences (Chapter Three). Invasive species abundance is often related to their impact on native species (Kumschick *et al.*, 2015; Latzka *et al.*, 2016), so in these riverscapes, spatial heterogeneity in flow disturbance that limited large trout densities likely mediated the strength of native–invasive interactions. In

light of these results, it was likely that confluence heterogeneity would also influence riverscape-scale temporal patterns in fish assemblages.

Heterogeneity at small spatial scales can lead to highly temporally variable communities, but at landscape scales temporal fluctuations in biotic assemblages are usually decreased by spatial heterogeneity (MykrÄ *et al.*, 2011; Schneck & Melo, 2013; McCluney *et al.*, 2014; Hovick *et al.*, 2016; Papanikolaou *et al.*, 2016). However, the influence of large-scale spatial heterogeneity on stability in the outcomes of native–invasive species interactions over time is unknown. I found low heterogeneity in flow disturbance around confluences was associated with higher temporal variation in the relative abundance of native and non-native fish species, supporting my second hypothesis. Higher temporal stability in native–invasive relative abundance around spatially heterogeneous confluences may have been supported by dispersal from abiotically distinct habitat patches.

Both metapopulation and metacommunity models suggest that dispersal can influence both population size and support large-scale species persistence in suboptimal or sink habitats (Hanski, 1999; Dala-Corte, Becker & Melo, 2017). Reduced spatial heterogeneity in habitats can increase temporal variation in biotic assemblages by homogenizing riverscape-scale ecological processes (McCluney *et al.*, 2014; Wilcox *et al.*, 2017), for example, by removing the potential for recolonisation or source–sink dynamics, (Brown *et al.*, 2011). Increased temporal stability in native–invasive species co-occurrence around high heterogeneity confluences, therefore, may have been facilitated by dispersal of individuals between spatially juxtaposed stable and disturbed stream branches. This movement was likely to have been bi-directional, with different processes operating on native galaxiids and introduced trout species. For example, while trout may generally be not as well adapted to flood disturbance as native fish species in New Zealand (Leprieur *et al.*, 2006; Woodford & McIntosh, 2011), in some

catchments they have high flood resilience (Jellyman *et al.*, 2017), possibly as a result of high riverscape heterogeneity via confluences providing access between stable streams and disturbed reaches for potential recolonists. Native non-migratory galaxiids, on the other hand, are severely affected by predatory trout (Townsend & Crowl, 1991; McDowall, 2006; McIntosh *et al.*, 2010, Jones & Closs, 2015), so tend to have higher densities in flood-disturbed streams, where trout abundances tend to be lower, and thus provide a refuge from competition and predation (Jellyman *et al.*, 2017). Disturbed streams are also harsh environments, however, so proximity to more stable conditions via confluences likely provides access for post-flood recolonists, resulting in higher and more temporally stable galaxiid abundance around heterogeneous confluences (Chapter Three). Temporal stability at large spatial scales, therefore, likely reflects population-specific responses to disturbance heterogeneity and spatially variable interspecific interactions.

Most freshwater heterogeneity research has examined species richness, citing increases in biodiversity downstream of confluence junctions (Osborne & Wiley, 1992; Fernandes, Podos & Lundberg, 2004; Kiffney *et al.*, 2006; Milesi & Melo, 2014), with species richness (alpha diversity) the most frequently used measure of community structure (Leibold, Chase & Ernest, 2017). However, recent meta-analyses conclude that the majority of assemblages experience no change in richness while they undergo compositional changes, such as I found, supporting the importance of relative abundance as a metric for detecting community change (Jones & Schmidt, 2017; Spaak *et al.*, 2017). In addition, while variability is rarely used as a response variable to assess the influence of disturbance, it can be a particularly sensitive metric that captures ecological responses often hidden by averaging (Fraterrigo & Rusak, 2008). Thus, my results linking assemblage stability with riverscape heterogeneity support the use of measures of temporal variability in community composition to provide important insights into the effects of landscape processes on communities.

My findings also have particular relevance for conservation and management efforts specifically directed towards ecologically significant characteristics of river networks. My results support the idea that preservation of heterogeneous riverscapes will encourage higher ecosystem resilience in the face of global change (Cromsigt, Prins & Olff, 2009; Flitcroft *et al.*, 2012; Wilcox *et al.*, 2017). Being able to identify mechanisms enhancing the stability of ecosystems, such as interactions between native and invasive species, is critical to do at spatial scales relevant for land management (Wilcox *et al.*, 2017). This is especially important when widespread homogenisation of riverscapes may be increasing temporal variability in native–invasive interactions, making assemblages more vulnerable to additional stressors such as climate change (Boddy & McIntosh, 2017). My findings suggest that maintaining riverscape-scale heterogeneity, by underpinning the buffering of assemblage stability, will likely enhance ecosystem resilience. My results also highlight the value of spatial heterogeneity associated with confluences for fish conservation at riverscape scales in invaded networks.

Plate 4. Surface water intake on Kowai River in the Canterbury Plains at high (top) and low (bottom) flow. At low flow most of the water was abstracted and the stream dried up just downstream of the intake.

Photos: Nixie Boddy

Chapter Five:

Big impacts from small abstractions: the effects of surface water abstraction on freshwater fish assemblages

Introduction

Freshwaters across the globe are increasingly manipulated through dewatering, water diversion, and water abstraction as anthropogenic demands grow and the effects of climate change become more pronounced (i.e., droughts and altered seasonality; Murchie *et al*., 2008). The modification of flow regimes is one of the most extensive anthropogenic alterations to lotic systems (Petts, 1984; Stanford, Ward & Liss, 1996) and is often cited as the largest threat to freshwater ecosystems (Naiman *et al.*, 1995; Sparks, 1995; Lundqvist, 1998; Ward, Tockner & Schiemer, 1999). Some estimates suggest that over 50% of the largest river systems worldwide are moderately or severely impacted by flow regulation (Dynesius & Nilsson, 1994; Nilsson *et al.*, 2005). Thus, the potential ecological impacts of this widespread flow modification are of major concern, however little is known about the effects of small abstractions, particularly on fish assemblages, aquatic food chains, and influences on native–non-native fish interactions.

River abstractions and diversions tend to modify natural flow patterns and cause fluctuations in discharge (Murchie *et al.*, 2008). Altering flows and abstracting water from rivers can often have negative impacts on the flora and fauna residing in and around them, and can lead to species declines and local extinctions (Bunn & Arthington, 2002; Dewson, James & Death, 2007b; Benda, Miller & Barquín, 2011). The effects of hydropower dams and large-scale diversions on aquatic communities have been well-documented (Poff & Zimmerman, 2010), but the impact of small abstractions on watercourses is understudied, despite being much more

common. For example, in New Zealand there are approximately 16,000 consented abstractions nationwide, with a mean water abstraction rate of 0.04 m^3/s, and 66% of these are for irrigation (Booker *et al.*, 2016), so understanding the cumulative impacts of small irrigation takes is critical to the management of freshwater systems. Even small in-stream takes such as surface water abstractions and v-notch gauging weirs can impact flow regimes and hydraulic connectivity (Pusey *et al.*, 1989; Bunn & Arthington, 2002), and thus mobile organisms such as fish. It is therefore important that the impacts of changes in flow regimes associated with small water abstractions on fish communities are well understood.

The relationship between flow regimes, habitat structure and fish communities has been well established (Poff & Allan, 1995; Hart & Finelli, 1999; Bunn & Arthington, 2002), so it is unsurprising that modifications to natural flow regimes, such as water abstractions, will change physical habitat and influence fish population structure (Bunn & Arthington, 2002). Most research on this subject has focused on abundance of target organisms (e.g., Leprieur *et al.*, 2006), or occasionally species diversity, but effects at the whole community or assemblage scale have received less attention. Habitat contraction as a result of decreased river flow has been associated with changes in community composition and abundance (Stubbington, Wood & Boulton, 2009; Datry, Arscott & Sabater, 2011), but understanding how trophic interactions respond to artificially decreased flows, could offer more insight into the processes driving these ecosystem shifts (McHugh *et al.*, 2014).

The directional flow component of river systems means the effects of water abstraction should vary upstream and downstream of the abstraction point, however this has not previously been specifically considered. If fish passage is blocked, migratory species often decline or disappear from upstream reaches (Harris, 1984; Bonetto, Wais & Castello, 1989; Joy & Death, 2001). Reaches downstream of an abstraction will also be influenced by reduced flow, and can

experience decreased fish abundance and maximum body size, and the loss of fluvial specialists in favour of generalist species (Haxton & Findlay, 2008; Ledger *et al.*, 2013; McHugh *et al.*, 2014). Therefore, we should expect distinct changes in fish community composition and relative abundance upstream and downstream of abstraction intakes. Some of these directional shifts in community composition could arise from changes in flow regime modifying native–non-native patterns of co-occurrence.

While native fish are adapted to natural flow regimes, modifications to natural flows can facilitate the invasion of non-native species potentially better adapted to altered flow conditions. Moreover, because conditions in anthropogenically-altered systems tend to be similar regardless of geographical location (Bunn & Arthington, 2002), this may result in homogenization of communities. Anthropogenic modifications often increase flow stability enabling introduced species to outcompete natives that are better adapted to high flow variability (Pusey *et al.*, 1989; Bunn & Arthington, 2002). We propose that for surface water takes, when a small proportion of the river is abstracted, flow could be moderated in favour of introduced species (Chen & Olden, 2017), however when a large proportion of the river is abstracted, the resulting increased risk of extreme low flow and drought events creates much harsher environmental conditions that will benefit the species best adapted to low flow extremes. Therefore, the balance of native and non-native species relative abundance will depend on which group is more sensitive to extreme flows, and how the environment has shaped the evolution of native fish traits. For example, in situations where non-native trout are more sensitive to flow loss than native galaxiids (Leprieur *et al.*, 2006) abstractions prevented trout from causing extirpations, thus flow abstraction could have a net benefit on native fish species if they are better adapted to extreme flow conditions than non-natives (Chen & Olden, 2017).

We examined the impact of small surface water abstractions, across a range of proportion of stream flow abstracted, on fish assemblages and derived metrics which reflected their functional and structural characteristics. These metrics included fish abundance, biomass, diversity, species richness, mass-abundance slope, maximum body size, carbon-range, food-chain length, and the ratio of native to non-native species abundance. Mass-abundance relationships derived from fish assemblage body-size relationships respond to habitat factors such as flood disturbance, flow, presence of predatory taxa, including non-native Salmonidae, and land cover (Layman *et al.*, 2005; Fraley *et al.*, 2018*).* Carbon range and food-chain length, measures of the breadth and height of trophic relations, respectively, can similarly be affected by many biotic and abiotic habitat factors (McHugh *et al.*, 2014; Fraley *et al.*, 2018).

We examined the effects of single-point surface-water abstractions using a spatially-extensive longitudinal sampling approach. This included sampling an array of stream reaches above and below abstraction points to account for inherent longitudinal variability along the watercourses, and to enable us to isolate the direct effects of single-point water abstractions from other trends associated with local hydrology. We hypothesized that the proportion of flow abstracted, possibly interacting with direction to abstraction point (upstream or downstream) and/or distance to abstraction, would affect fish assemblage characteristics such as abundance and biomass (*H1*). This would potentially be due to effects of abstractions on directional connectivity, barriers to movement, and reductions in physical habitat size or productive space due to loss-of-flow. We expect that distance to abstraction location may be important due to a "shadow" effect of the abstraction on biota, with groundwater recharge potentially mitigating flow loss further away from the abstraction point. We also predicted that the ratio of native to non-native species abundances would change, particularly downstream, with higher proportional native abundance in downstream sites with flows unsuitable for large-bodied non-native trout (*H2*). Finally, we posited that stable isotope-derived measures of trophic breadth,

such as food-chain length and carbon range, would be similarly affected by flow abstracted, and direction and distance to abstraction (*H3*). Here we expected a loss of fish abundance and diversity would lead to fewer feeding options for biota, and thus a narrower prey range and decreased number of trophic links in reaches with high rates of flow abstraction.

Methods

Study site

One of the challenges of this type of study is the separation of direct effects of the modified flow regime from impacts associated with land-use change and intensification that are often associated with the development of such water resources (Bunn & Arthington, 2002). New Zealand is an ideal study system as the headwaters of many foothill and mountain rivers remain relatively unimpacted by land conversion. Thus, we could target surface water abstraction sites on streams with unimpacted headwaters and large riparian buffers to minimise the confounding influences of land-use change and identify the direct effects of water abstractions on fish communities.

Four surface water diversions (termed 'sites') were surveyed in the Canterbury foothills, New Zealand. These abstractions were selected to incorporate a gradient of proportion of flow abstracted, and to include both dammed and undammed surface water diversions. All sites were subject to similar climatic conditions, distance to the ocean, and regional species pool (based on information from the New Zealand Freshwater Fish Database; McDowall & Richardson, 1983), and all had relatively unimpacted catchments upstream of the abstraction point. To separate abstraction-related patterns from longitudinal stream trends, we structured our sampling reaches by splitting them into two sections: ten reaches upstream of the abstraction point, and five reaches downstream (Fig. 5.1). A higher number of reaches were included upstream of the abstraction point to quantify natural flow variation and fish assemblage

fluctuations for comparison with downstream abstraction-affected reaches. The length of each sampling reach was five times the stream width, and the distance between reaches was five times the average reach length for that section. Reach lengths were a constant multiple of mean stream width to avoid incorporating variability due to sampling different proportions of available habitat (Peterson & Ver Hoef, 2010). Reach lengths of five times the stream width were deemed sufficient to represent the habitat complexity in smaller streams, yet were not so large that reaches at larger streams were unachievable to sample in a day.

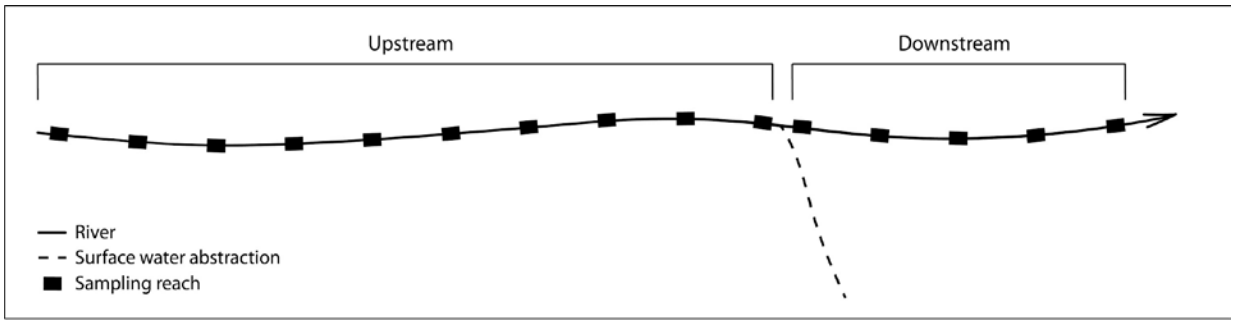

Fig. 5.1: Schematic diagram of longitudinal sampling reaches around a surface water abstraction point. Ten reaches were sampled above the abstraction and five downstream. Each reach length was five times the average stream width, and distance between reaches was five times the reach length.

Habitat measurements

Seven habitat characteristics were identified as being potentially ecologically significant and measured for inclusion in analyses: Pfankuch River Disturbance Index (RDI), substrate size, stream width, depth, discharge, macrophyte cover and reach flow characteristics. Discharge was calculated at one transect per reach using the velocity-area method to create a cross-sectional discharge profile at each of five reaches evenly-spaced along the longitudinal gradient at each site (including directly above and below the abstraction point), and linear interpolation was used to derive flow for the reaches in-between. From discharge data, we calculated the proportion of maximum flow (%Flow) for each reach within each site as a proxy variable for effects of abstraction and any additional lateral or vertical flow exchanges between stream water and groundwater. Wetted width and water depth were measured along one transect at each reach. RDI, which is calculated by summing 15 aspects of channel morphology from the stream bed and banks to evaluate physical habitat stability and flood-proneness of a river channel (Pfankuch, 1975; McHugh, McIntosh & Jellyman, 2010; Jellyman, Booker & McIntosh, 2013), was scored at every reach by the same person to ensure consistency. The percentage of the reach consisting of cascade, riffle, run, and pool meso-habitat types (Maddock, 1999) and the percentage area cover by in-stream macrophytes was estimated visually. The Wolman Walk method was used to calculate mean substrate sizes from 50 randomly selected substrate particles measured along the beta axis (Green, 2003). We also identified whether each stream reach was upstream or downstream of the abstraction point, and measured the distance from the abstraction point (Ups and DistA respectively; Table 5.1).

Table 5.1: Predictor and response variables evaluated in quasi-Poisson generalized linear models. Responses were converted to count data (multiplied by 1000) for purposes of rescaling and to fit our Poisson modelling framework, except for mass-abundance slope (kept untransformed for use in a linear model). See methods for detailed description of datasets and variables.

Type	Variable	Abbreviation	Units	Reference
Response	Abundance per metre reach length	Abundance	fish/metre	N/A
	Median body mass	Median	grams	N/A
	Biomass per metre reach length	Biomass	grams/metre	N/A
	Shannon diversity index	Shannon	unitless	Weaver & Shannon (1949)
	Ratio of native fish abundance to trout abundance	Native–trout ratio	unitless	N/A
	Mass-abundance relationship slope	Mass-abundance slope	unitless	Jennings *et al.* (2002)
	Mass-abundance relationship slope (extreme %Flow values only)	Mass-abundance slope (extremes only)	unitless	N/A
	Food-chain length (Δ δ15N)	FCL	unitless	Post *et al.* (2000)
	Carbon range (Δ δ13C)	Crange	unitless	McHugh *et al.* (2014)
Predictor	Proportion of maximum stream flow (stream-specific)	%Flow	%	N/A
	Upstream or downstream from abstraction point	Ups	2-level factor	N/A
	Distance from abstraction point	DistA	metres	N/A
	Abstraction site identity	StreamID	4-level factor	N/A

Fish capture and processing

Fish were caught using single-pass electrofishing conducted downstream into a push net using a Kainga EFM 300 backpack electrofishing machine (NIWA Instrument Systems, New Zealand) generating pulsed DC current. Single-pass electrofishing catch efficiency was verified through comparison with standard quantitative three-pass electrofishing using stop nets in a separate investigation to ensure that metrics generated were comparable (Fraley *et al.*, 2018). Fish were anaesthetized using AQUI-S^{TM} 20E (AQUI-S New Zealand Ltd.), counted, measured for total or fork length (species-dependent, mm), and each individual was identified to species. Six fish of representative taxa and sizes (spanning the smallest, medium, and largest) from each location were euthanized (if <400 mm TL) with an overdose of AQUI-S fish anaesthetic and frozen, or a non-lethal fin clip was taken (if >400 mm TL; Sanderson *et al.*, 2009) and frozen for later stable isotope (SI) processing in the laboratory.

Fish assemblage and native–introduced ratio metrics

Fish mass (g) was calculated from field-measured total or fork length (depending on species morphology), using regressions relating fork length, total length, and mass of New Zealand fish species (Jellyman *et al.*, 2013). A subset of fish euthanized for this study were measured in the field and weighed in the laboratory to verify the applicability of these published relationships (R^2 > 0.95 for all species). Additionally, to construct mass-abundance relationships (also known as size spectra), individual fish mass was log-transformed and binned in even steps along a $\log_{10}$ scale to best fit the range of fish body sizes at our reaches, and abundance of fish in each bin was also $\log_{10}$-transformed. A linear regression was constructed relating $\log_{10}$ binned abundance to the midpoints of $\log_{10}$ binned fish mass, and the slope was extracted to use as a response variable (mass-abundance relationship slope, Table 5.1; Jennings *et al.*, 2002; Fraley *et al.*, 2018). Other responses were calculated for fish assemblages in each

reach, including: Shannon-Weaver diversity index (Weaver & Shannon, 1949), median fish body mass (B50; g), total biomass (g/m), and abundance (no. fish/m; Table 5.1). Additionally, we calculated simple abundance and biomass ratios between native fishes and introduced brown trout (*Salmo trutta*), the only non-native species present, to see if abstractions differentially affected native and non-native fishes. Responses were converted to count data (multiplied by 1000) for purposes of rescaling and to fit our Poisson modelling framework, except for mass-abundance slope and native–introduced ratios (kept untransformed for use in linear models).

Stable isotope preparation and analysis

Primary consumers (*Deleatidium* spp. mayflies) were collected using a kick-net at each of the five reaches sampled for discharge (netted from three or more locations within each reach), and frozen for transport back to the laboratory. *Deleatidium* were chosen as a baseline consumer because they are ubiquitous in New Zealand, were present at all abstraction sites, and are commonly utilized by fishes as prey (Fraley *et al.*, 2018). Primary consumers were utilized as a baseline to compare with fish for SI food-chain length analysis (McHugh *et al.*, 2012). In the laboratory, *Deleatidium* from each reach were dissected and the stomach contents and head removed to eliminate potential bias from SI values (Lancaster & Waldron, 2001). Composite *Deleatidium* samples were gathered from 20–100 individuals from each reach, following methods for composite samples from Post (2002). Fish were dissected and a portion of dorsal muscle tissue was extracted, or fin tissue was substituted for individuals >400 mm to avoid lethal sampling (Hanisch *et al.*, 2010). Next, fish and invertebrate tissues were dried in an oven for at least 72 hours at 50 °C, then ground into a fine powder using a mortar and pestle, with care taken to avoid contamination. Approximately 2 mg of powder from each sample was placed in an 8 × 5 mm tin capsule, folded, and sent to the University of California-Davis Stable

Isotope Facility for analysis through isotope ratio mass spectrometry (on a PDZ Europa 20-20; Sercon Ltd.).

The resulting nitrogen isotope ratios were used to calculate trophic position (TP) of the sample organism, using an equation from Post (2002), as applied to similar streams by McHugh *et al.* (2012). The highest fish TP value from each reach was used as an estimate of food-chain length for the reach. Carbon isotope values were corrected for lipid content using established relationships (Post *et al.*, 2007). Carbon isotope ratio range was calculated for fishes from each reach following an equation from (McHugh *et al.*, 2014). For brown trout it was not necessary to correct fin clip SI values to muscle values per McCarthy and Waldron (2000), who found no significant differences between tissue types for this species, but corrections were needed for fin clips from the only other species >400 mm found in our study area, longfin eel (*Anguilla dieffenbachii*).

Data analysis

We evaluated the relationship between responses (*H1*: fish abundance, mass-abundance slope, biomass; *H2*: native–introduced abundance ratio; and *H3:* FCL, and Crange) and predictor variables (%Flow, Ups, DistA) using reaches within abstraction sites as replicates (Table S1). Non-collinearity of predictors was verified by calculating variance inflation factors (VIF; cutoff ≥ 5), and some predictors originally tested (including RDI, Wolman Walk substrate size, macrophyte cover, stream depth, and wetted width) were eventually removed from models to eliminate overfitting or because they did not contribute to explaining variance in the data. The distance from abstraction variable (DistA) was scaled (centered and transformed to have a similar range to other variables) to eliminate issues in model fitting. A saturated quasi-Poisson generalized linear model was constructed for most response variables (except for mass-abundance and native–introduced abundance ratio) using the (glm) function in R version 3.4

(R Development Core Team, 2016). Quasi-Poisson models, fitted using the 'quasipoisson' link in the 'glm' function, were used to deal with the overdispersion present in standard Poisson models (Zeileis, Kleiber & Jackman, 2008). Simple linear models using the 'lm' function were constructed for mass-abundance slope and native–introduced abundance ratio responses. Models with various interactions between predictors were compared to evaluate the importance of proportion of flow remaining (%Flow), distance from abstraction (DistA), and direction to abstraction (upstream or downstream; Ups) on fish assemblages, and to test all hypotheses. A term, including a variable identifying the stream sampled (StreamID), was included in each model (StreamID * Ups + DistA; Table 5.1) to account for our nested study design and structure the degrees of freedom to reduce the possibility of Type I errors (Dormann *et al.*, 2007). Using analysis of deviance for 'glm' models and analysis of variance for 'lm' models (ANOVA), predictors within the global model for each response were evaluated for significance ($\alpha < 0.05$). Pseudo R^2 (McFadden's R^2; Faraway, 2016) was also calculated for each response to assess goodness-of-fit of the saturated model compared to that achieved by a null model including a single parameter representing the intercept term. For analysis of the mass-abundance slope predictor, we also constructed a model assessing only reaches with the lowest and highest %Flow values upstream and downstream of the abstraction point at each site to minimize noise in the data occurring when all reaches were included in the original mass-abundance model. Four downstream reaches at the Kowai River site had 100% flow loss and no fish present, and these were omitted from our analyses. The entire Kowai site was also removed for the mass-abundance slope analysis because there was only one downstream reach that had water and we required both minimum and maximum flow reaches for our analysis. Partial effects plots of the model results were produced using the 'ggplot2' (Wickham, 2009) and 'effects' (Fox, 2003) packages in R.

Results

Site and habitat characteristics

Some predictors originally tested (including RDI, Wolman Walk substrate size, macrophyte cover, stream depth, and wetted width) were removed from models to eliminate overfitting or because they did not contribute to explaining variance in fish assemblages. Of the four abstraction sites sampled, a marked decrease in flow occurred downstream of the abstraction point in three sites, with flow increasing in Taylors Stream due to a drain input just upstream of the abstraction (Fig. S1). Average discharge at the time of sampling ranged from <0.01 m^3/s in the smallest waterway (Limestone Creek) to 0.87 m^3/s in the largest waterway (Taylors Stream; Table S1), and percentage of total flow loss from abstraction and downwelling varied between 57% in Taylors Stream to 100% in the Kowai River (where four of the reaches downstream of the diversion were dry). River Disturbance Index, averaged per site, ranged from 65 (low flood disturbance) in Limestone Creek to 116 (high flood disturbance) in the Kowai River, thus our sites encompassed a range of natural flood disturbance regimes.

Fish assemblages

The 4,457 fish caught, included native Canterbury galaxias (*Galaxias vulgaris*), upland bully (*Gobiomorphus breviceps*), longfin eel (*Anguilla dieffenbachii*), torrentfish (*Cheimarrichthys fosteri*), and introduced brown trout (*Salmo trutta*), with species richness varying among reaches from one to five taxa (Table S1). The most ubiquitous species across sites were *G. breviceps* and *G. vulgaris* (present at all four sites), while *C. fosteri* were least widespread (only one site). Across sites, the most abundant taxa were *G. breviceps* (72.1% of total catch) and *G. vulgaris* (21.2%), and the most uncommon were *A. dieffenbachii* (0.1%) and *C. fosteri* (0.2%). Total fish biomass across sites was dominated by *S. trutta* (42.8%) and *G. breviceps* (25.9%), with *C. fosteri* (< 0.1%) and *G. vulgaris* (13.1%) contributing the least. Given the rarity of

native predatory fish (longfin eels) in these systems, non-native trout were an important predator in these fish assemblages.

Quasi-Poisson models predicting fish assemblage metrics performed substantially better than the null models in most cases (pseudo-$R^2 > 0.5$; Table 5.2), with the exception of fish biomass (pseudo-$R^2 = 0.17$). The linear model (not quasi-Poisson) predicting mass-abundance slope had poor explanatory power (adjusted $R^2 = 0.08$), however the mass-abundance model including only reaches with the lowest and highest %Flow upstream and downstream of the abstraction points performed much better (adjusted $R^2 = 0.65$).

ANOVA indicated that %Flow and Ups factors interacted to significantly affect fish abundance and the mass-abundance relationships (for lowest and highest flow reaches) at our abstraction sites (Table 5.3; Figs. 5.2, 5.3). This indicated that the number of individuals per metre of stream length, and the size structure and abundance within the assemblage, were significantly influenced both by the amount of water abstracted and the direction from the abstraction point (supporting *H1*).

Upstream of the abstraction point, fish abundance did not vary with decreasing proportion of maximum flow (Fig. 5.2). Downstream however, abundance declined with decreasing %Flow, and downstream reaches with high %Flow contained higher fish abundances than reaches with equivalent flows upstream (Fig. 5.2; Table 5.3). Natural flow fluctuations modified flow upstream of abstractions by up to 50%, however no significant change in fish abundance per metre of stream length was seen associated with this natural flow variability. Similarly, with mass-abundance slope (for highest and lowest %Flow upstream and downstream at each site), there was minimal change in the relationship upstream of the abstraction; a slightly increasing mass-abundance slope did indicate a shallower (but negative) distribution of fish size class abundance (Fig. 5.3). However, downstream of the abstraction, the slope became more steeply

negative. The driver of this interaction was the loss of larger-bodied size-classes of fish with decreased flow in downstream reaches (See Fig. S2 for visualization of this). There was no evidence of an additional significant interaction between %Flow, Ups, and for any of the response variables, nor was DistA a significant main effect.

Native–introduced fish relative abundance

Fish assemblages were numerically dominated by native fish (from 6 to 33 times more abundant), and for the three abstraction sites sampled where non-native brown trout were present, they comprised between 1.3 to 5 times more biomass (Limestone Creek did not contain any trout; Table S1). At the two sites where trout were present and with suitable replication of reaches both upstream and downstream of abstraction (Taylors Stream and Pudding Hill Stream), native fish abundance increased relative to trout with decreased %Flow both upstream and downstream of abstraction points (Table 5.3; Fig. 5.4). The relationship, however, was much stronger in downstream reaches, with rapid decreases in co-occurrence as local flow declined. Interestingly, at the downstream reaches at both sites, the largest fish in reaches with highest %Flow were brown trout, while the largest fish in reaches with lowest %Flow were native taxa. Our linear model predicting the relative abundance of native and introduced fish explained variance in the data well (adjusted R^2 = 0.60; Table 5.2), underscoring the explanatory power of flow and habitat size in determining the outcome of interactions between native and introduced taxa.

Table 5.2: Characteristics of saturated quasi-Poisson generalized linear models for fish assemblage responses. The nested study design was accounted for with a StreamID*Ups + DistA term in all models (not presented here; see text for explanation). See Table 1 and Methods for explanation, coding, and units of variables. Pseudo R^2 refers to McFadden's pseudo R^2, which is a comparison of goodness-of-fit between the saturated model (as presented in this table) and a null model with only an intercept term.

Response	Structure	Degrees of freedom (null)	Residual deviance (null)	Psuedo R^2
Abundance	Ups * %Flow	45 (55)	27 (154)	0.82
Biomass	Ups * %Flow	46 (55)	620 (738)	0.16
Shannon	Ups * %Flow	46 (55)	3561 (7434)	0.52
Native–trout ratio*	Ups * %Flow	23	7.43	0.60
Mass abundance slope*	Ups * %Flow	46	0.32	0.04
Mass abundance slope* (extremes only)	Ups * %Flow	3	0.21	0.65
FCL	Ups * %Flow	45 (55)	682 (1094)	0.38
Crange	Ups * %Flow	46 (55)	26049 (37129)	0.30

*The models for mass-abundance slope and native–trout ratio are simple linear models (not quasi-Poisson glm like the others) and the residual standard error and adjusted R^2 are shown in place of residual deviance and pseudo R^2, respectively.

Table 5.3: Analysis of deviance and variance, and summary output for quasi-Poisson generalized linear models ('glm') and simple linear models ('lm') for fish assemblage responses. Model structure is specified in Table 2. Responses were converted to count data (multiplied by 1000) to fit our Poisson modelling framework, except for mass-abundance slope, which used a linear model. See Table 1 and Methods for explanation, variable definitions, and units of variables.

Response	Predictor	Estimate (std. error)	F-value	P value
Abundance	Ups*%Flow	-1.64 (0.70)	5.57	0.02
	%Flow	1.90 (0.51)	17.69	<0.01
	Ups	3.18 (2.06)	19.81	<0.01
	DistA	-0.24 (0.10)	1.12	0.3
Biomass	%Flow	-0.03 (1.06)	0.77	0.38
	Ups	4.31 (8.58)	0.07	0.79
	DistA	-0.16 (0.20)	0.94	0.34
Shannon	%Flow	0.33 (0.32)	0.48	0.49
	Ups	0.14 (0.42)	0.13	0.72
	DistA	-0.01 (0.06)	0.03	0.86
Native–trout ratio*	Ups*%Flow	-134.34 (38.55)	12.14	<0.01
	%Flow	16.89 (13.76)	1.32	0.26
	Ups	20.68 (12.05)	2.8	0.11
	DistA	3.96 (2.42)	4.1	0.05
Mass-abundance slope*	%Flow	-0.15 (0.29)	0.98	0.33
	Ups	0.04 (0.20)	2.61	0.11
	DistA	0.03 (0.06)	0.01	0.93
Mass-abundance slope* (extremes only)	Ups*%Flow	-2.35 (0.58)	3.2	0.03
	%Flow	0.64 (0.37)	0.52	0.52
	Ups	1.19 (0.47)	3.2	0.17
	DistA	0.03 (0.12)	0.08	0.79
FCL	Ups*%Flow	0.34 (0.14)	5.64	0.02
	%Flow	-0.09 (0.07)	<0.01	0.95
	Ups	0.10 (0.08)	4.59	0.04
	DistA	-0.01 (0.01)	2.01	0.16
Crange	%Flow	0.19 (0.38)	0.05	0.82
	Ups	1.12 (0.41)	2.9	0.1
	DistA	-0.01 (0.01)	0.23	0.63

*The models for mass-abundance slope and native–trout ratio are simple linear models (not quasi-Poisson glm like the others).

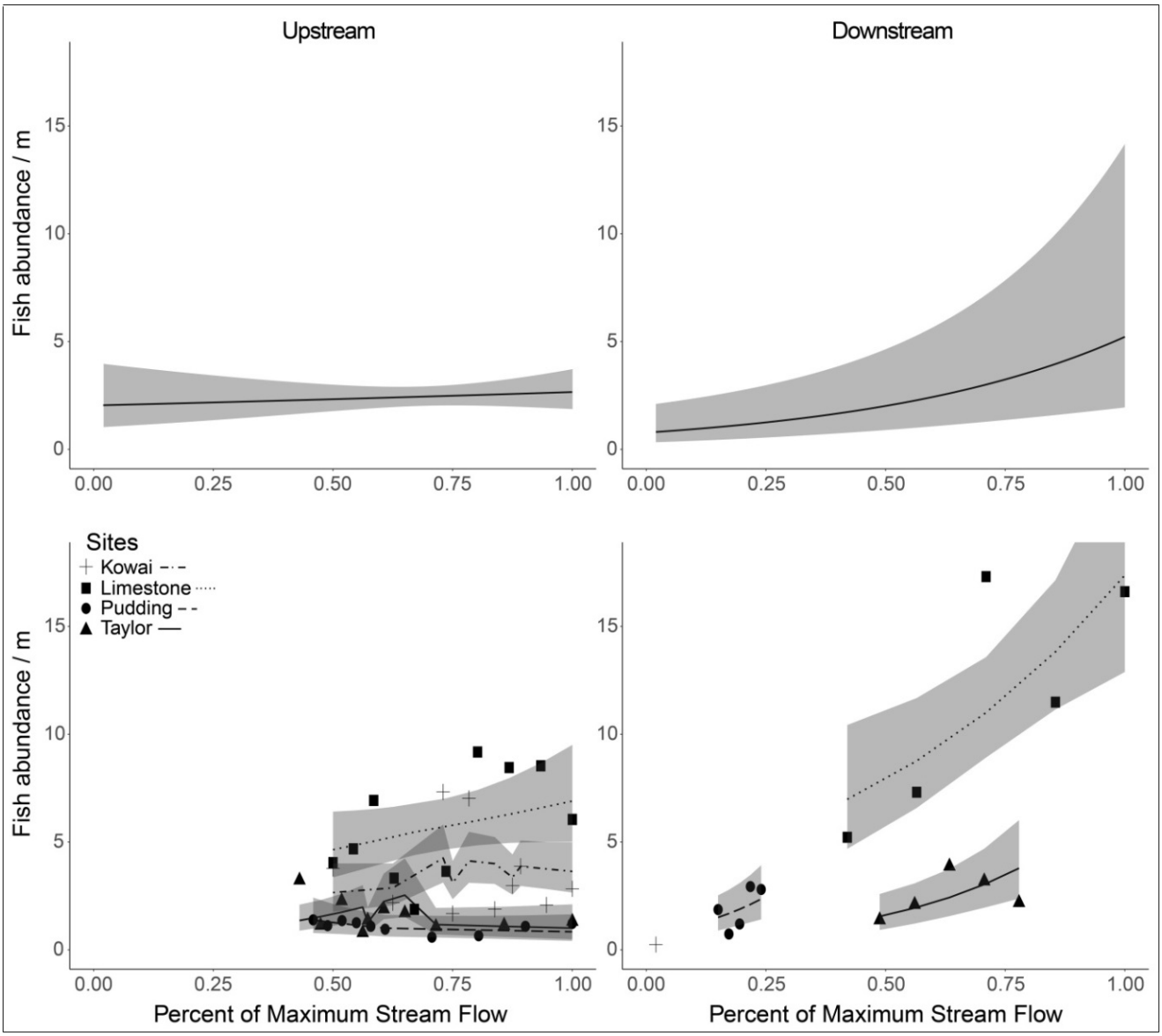

Fig. 5.2: Total fish abundance per metre of stream length, depending on proportion of maximum stream flow and direction to abstraction (upstream or downstream). Top panels show partial effects plots and bottom panels show predicted and raw values for each stream. Predicted lines in the bottom panel will not necessarily be smooth because each prediction is influenced by the observed points' distance to confluence. Lines represent model estimates with 95% confidence intervals displayed as grey bands. Points show raw data with shapes representing the site each sample was taken from. See Table 1 for explanation of variable derivation and units, and Table 3 for statistical values.

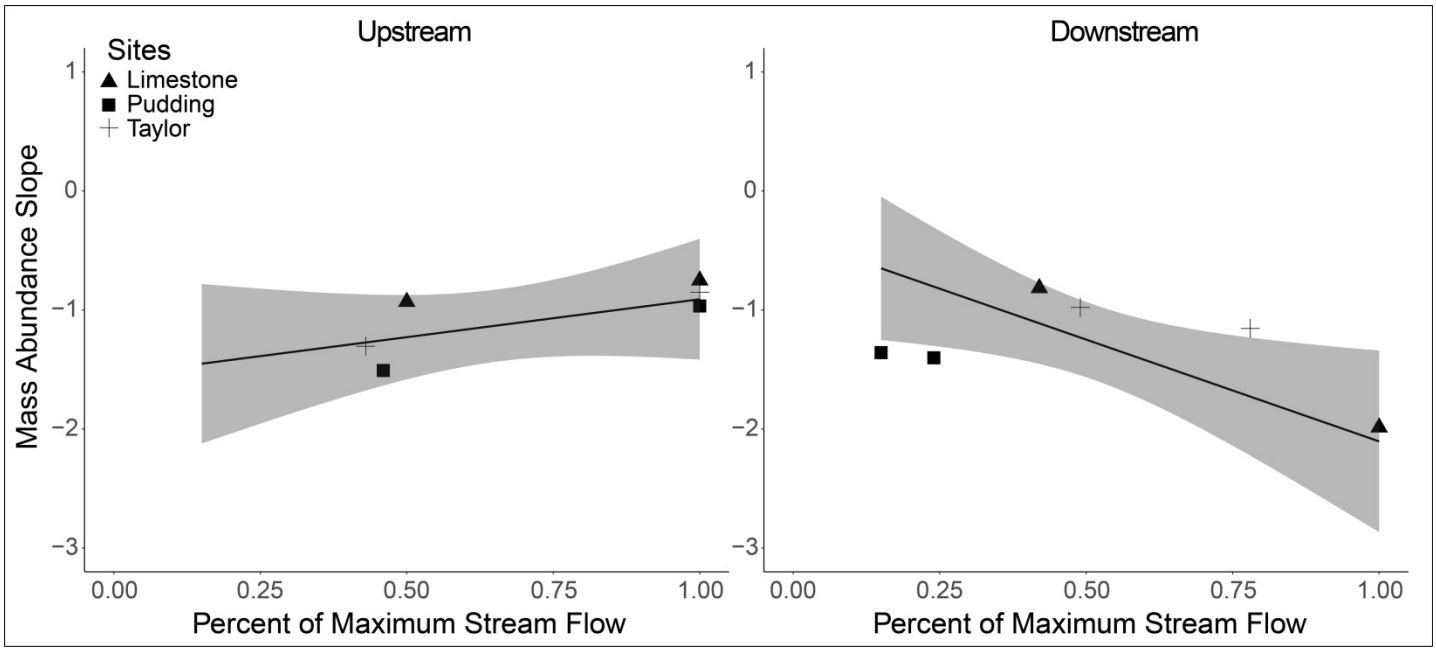

Fig. 5.3: Partial effects plots showing significant interactions between proportion of maximum stream flow and direction to abstraction (upstream or downstream) on mass-abundance slope for a subset of stream reaches at each site. Lines represent model estimates with 95% confidence intervals displayed as grey bands. Points show raw data with shapes representing sites. The subset is limited to the reaches which have the lowest and highest %Flow values upstream and downstream at each site. The Kowai River site is not included because only one reach downstream of the abstraction contained fish. See Table 1 for explanation of variable derivation and units, and Table 3 for statistical values.

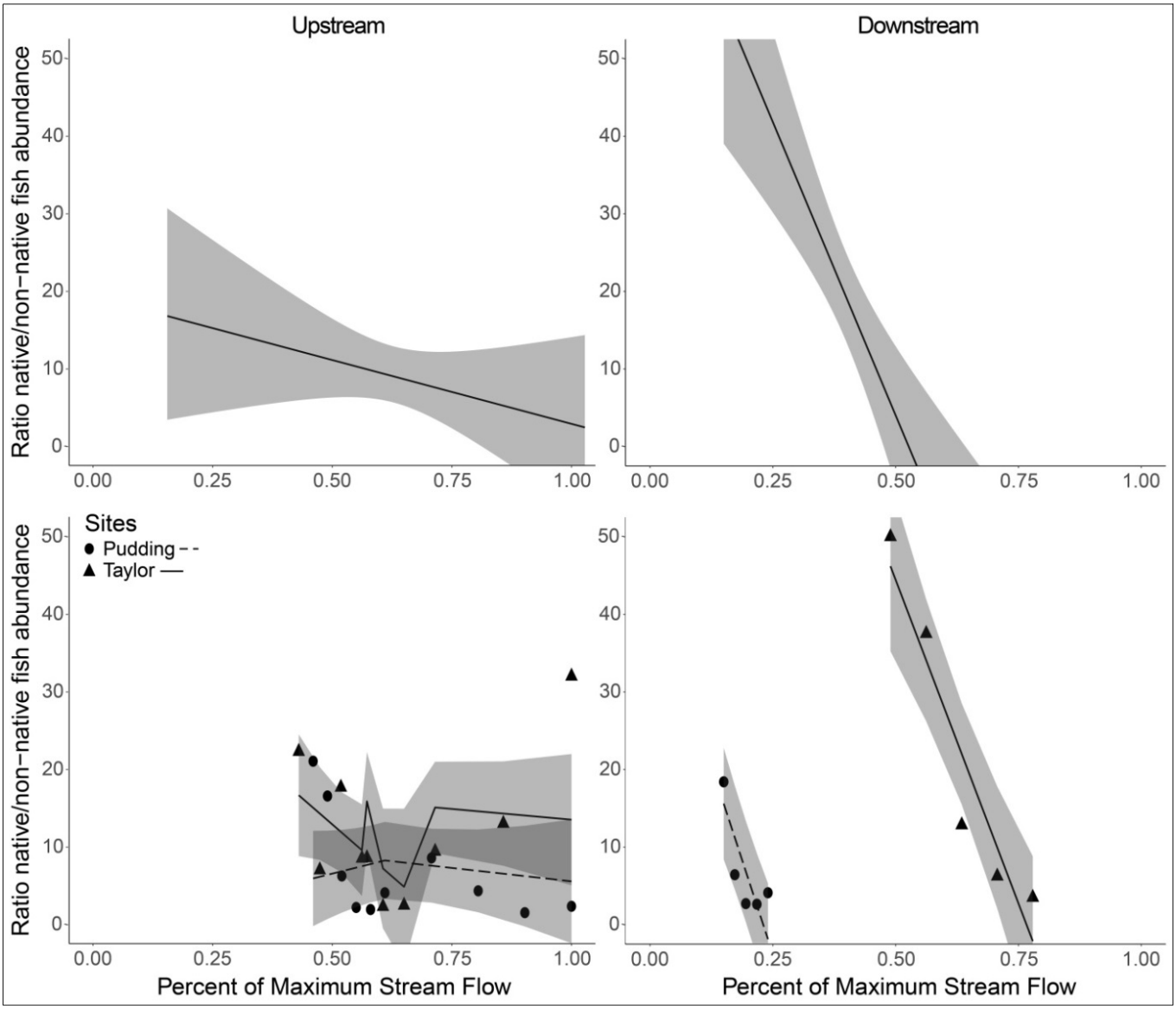

Fig. 5.4: Proportion of the fish assemblage that was native compared to non-native, depending on a significant interaction between proportion of maximum stream flow and direction to abstraction (upstream or downstream). Top panels show partial effects plots and bottom panels show predicted and raw values for each stream. Predicted lines in the bottom panel will not necessarily be smooth because each prediction is influenced by the observed points' distance to confluence. Lines represent model estimates with 95% confidence intervals displayed as grey bands. Points show raw data with shapes representing sites. The Limestone River site was not included because no non-native fish were captured at any reach, and the Kowai River site was not included because the reach downstream of the abstraction did not

contain non-native fish. See Table 1 for explanation of variable derivation and units, and Table 3 for statistical values.

Food-chain length and carbon range

Relative to fish assemblage metrics, quasi-Poisson models relating stable isotope-derived metrics to proportion of flow abstracted did not explain as much variance (pseudo-$R^2 < 0.4$; Table 5.2). No significant relationships were found with carbon range predictors, indicating little change in trophic breadth (Table 5.3). However there was a significant interaction between %Flow and position upstream or downstream of the abstraction affecting food-chain lengths, with decreases in FCL downstream of abstractions. Thus, abstractions did influence stable isotope-derived metrics downstream, by reducing the number of trophic links in the fish assemblage when higher proportions of the flow were removed (supporting *H2*).

Food-chain length increased with decreasing proportion of flow upstream of abstractions (supporting *H3*). The effect was inverted downstream, and trophic changes were much steeper, indicating food chains rapidly decreased in length as local flow decreased (Fig. 5.5). This was driven primarily by a loss of larger-bodied fish (Fig. S2), typically brown trout at the top of the food chain, in downstream reaches with lower local flow. Overall food-chain lengths in these systems were highly variable, as the weak model fit suggests. There was no evidence of an additional significant interaction between %Flow and Ups for any of the response variables, nor was DistA a significant main effect.

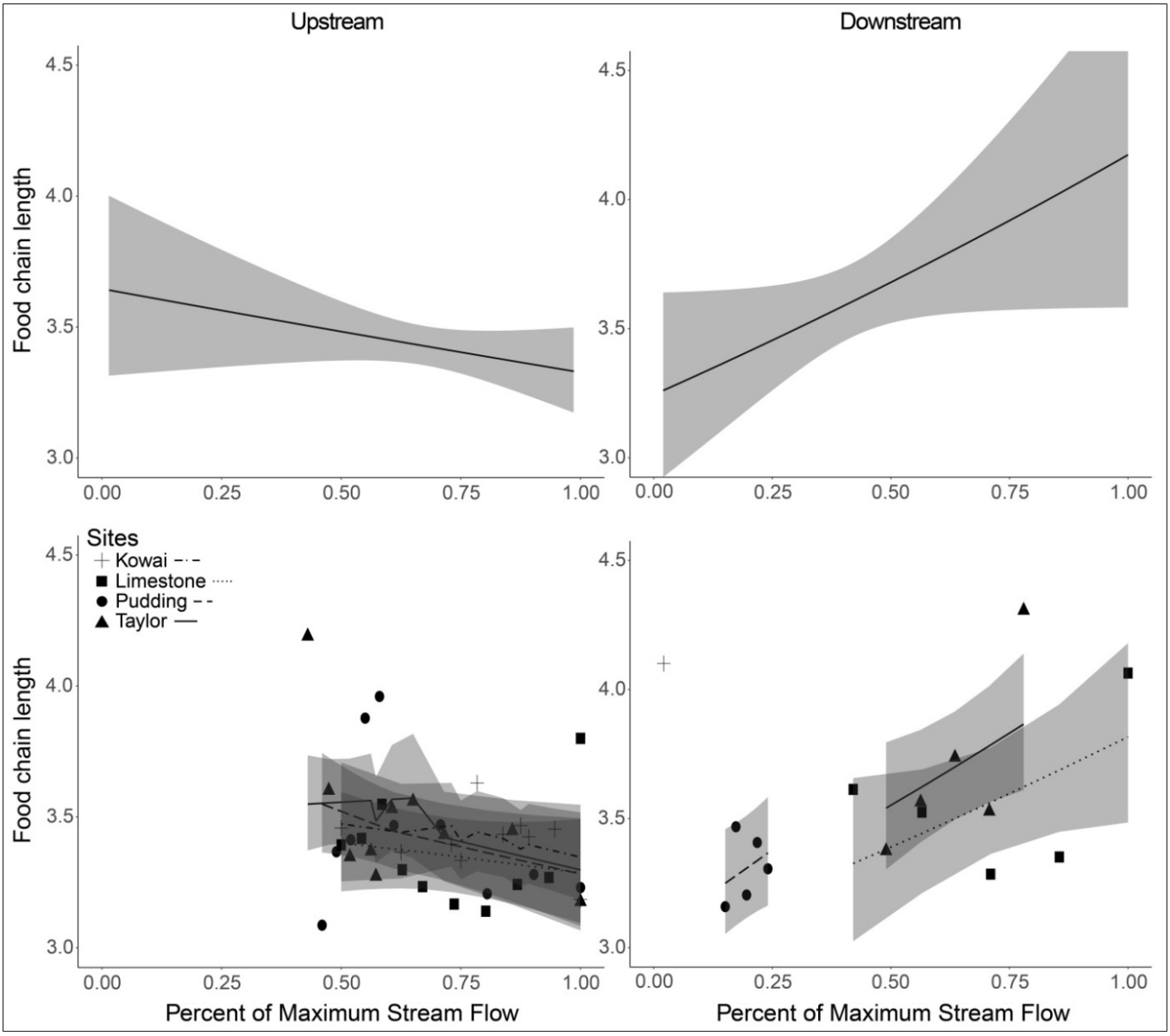

Fig. 5.5: Food-chain length, depending on proportion of maximum stream flow and direction to abstraction (upstream or downstream) on food-chain length. Top panels show partial effects plots and bottom panels show predicted and raw values for each stream. Predicted lines in the bottom panel will not necessarily be smooth because each prediction is influenced by the observed points' distance to confluence. Lines represent model estimates with 95% confidence intervals displayed as grey bands. Points show raw data with shapes representing the site each sample was taken from. See Table 1 for explanation of variable derivation and units, and Table 3 for statistical values.

Discussion

Recognition that anthropogenic alteration of flow regimes is a threat to aquatic ecosystems globally has led to increasing interest in understanding the responses of aquatic ecosystems to different types and degrees of flow alteration (Dudgeon *et al.*, 2006; Poff & Zimmerman, 2010). Only a handful of studies in temperate-region rivers have examined the effects of small abstractions, with widely varying conclusions. Several of these projects found little or no detrimental impact of abstraction on the study organisms (Leprieur *et al.*, 2006; Dewson, James & Death, 2007a; Lange *et al.*, 2014), while others found negative effects on the abundance and diversity of organisms downstream of abstraction (Death, Dewson & James, 2009; Matthaei, Piggott & Townsend, 2010; Falke *et al.*, 2011). Our investigation showed that flow loss downstream of surface water abstractions significantly affected fish abundance, mass-abundance slope, food-chain length, and relative abundance of native and introduced fishes. As we expected, these effects depended on spatial position relative to the abstraction point, with downstream reaches affected to a greater degree than upstream areas. However, there was no additional interaction with distance from the abstraction point as we hypothesized. Given the high proportion of rivers globally that are potentially impacted by small abstractions (Anderson, Freeman & Pringle, 2006; Deitch, Kondolf & Merenlender, 2009), the effects they can have on fish assemblages, such as those outlined below, are likely to be extremely influential.

Effects of water abstraction on fish assemblages

Abstractions likely affected fish assemblages through reduced quantity and quality of physical habitat associated with decreased wetted width, depth and water velocity, possibly by prevention or interruption of fish movement upstream or downstream of diversion points. As predicted in *H1*, fish abundance was lower below abstraction points when flow loss was high,

and mass–abundance relationships (at extreme %Flow values at each reach) had steeper slopes. In terms of abundance, the loss-of-flow downstream of abstraction points typically resulted in smaller habitat sizes, potentially reducing carrying capacity for fishes, but no statistically significant decreases in biomass or fish diversity were detected. For mass-abundance slope, reaches with the highest %Flow downstream of abstractions had higher abundance of small-bodied fish but larger-bodied size classes were absent. This may be caused by large-bodied fish, such as trout, leaving abstraction-exacerbated low flow reaches, while small-bodied native fishes such as galaxiids and bullies either remained because they were less affected (similar to findings of Leprieur *et al.*, 2006), or possibly were released from predation by trout. Similar research from tropical Central America found that fish assemblages, but not abundance, changed in composition upstream and downstream of abstraction sites on small, mountainous streams (Anderson, Freeman & Pringle, 2006), unlike our results which showed significant changes in both of those metrics.

Using our longitudinal sampling design, we were interested in how fish assemblage structure changed in relation to natural flow variation, due to upwelling and downwelling, compared to artificial changes in flow associated with abstractions. Surface water-groundwater interactions such as these are common in many rivers globally that have large gravel floodplains (Brunke & Gonser, 1997). The significance of the interaction between proportion of flow loss and direction (upstream or downstream) from the abstraction point indicates that the assemblage composition and the relative abundance of different size-classes of fish were only affected by loss-of-flow caused by the artificial abstraction, and not by natural fluctuations in flow caused by groundwater losses or gains. Flow loss caused by abstraction can be clearly visualized and compared with variability resulting from groundwater losses or gains in Fig. S1. These results suggest there is a fundamental difference in a fish assemblages' ability to cope with and respond to natural versus anthropogenic flow variation.

One of our abstraction sites (Limestone Creek) had a partial fish movement barrier associated with the abstraction, and all sites had diversion channels without fish exclusion devices, in which fishes could become entrained, which may explain some of the interacting effects of flow loss and flow direction from the abstraction point. While these diversion channels were not flowing at high velocity, it would be easy for downstream-migrating fishes to choose to swim into them, which could result in disorientation or mortality due to desiccation or water intake machinery (e.g., pumps), depending on the terminus of these channels. This may be a particularly important mechanism when a high proportion of river flow is being extracted, which may be associated with the low abundances we found at low proportion-flow sites. A similar project looking at abstractions in Puerto Rico, USA found that freshwater shrimps similarly increased in abundance downstream of a small dam that was a partial migration barrier, and that up to 100% of downstream-migrating shrimp larvae were entrained into the intake of the associated abstraction (Benstead *et al.*, 1999). While we did not monitor entrainment of fishes into the surface-water intakes we were examining, this would be a useful future avenue of research to explain the mechanisms behind upstream-downstream differences in fish communities.

Effects on native and introduced species

Similar to predictions in *H2*, there were higher numbers of native fishes at reaches with greater flow loss from abstraction, relative to numbers of introduced brown trout. Unlike trout, New Zealand native fishes are adapted to living in smaller, often benthic habitats, and in the case of galaxiids, even occupying streambed interstitial spaces (Davey, Kelly & Biggs, 2006). For example, the reaches we sampled downstream of the abstraction on the Limestone Creek consisted of very shallow water flowing through rock matrices, yet they were populated by hundreds of upland bullies. Thus, native fish could have higher relative abundances

downstream of abstractions either due to the absence of trout (less predation and competition) or due to a preference for the habitat characteristics caused by the abstractions. However, this does not necessarily mean native fish were thriving in these areas of flow loss, because they may have also been negatively impacted, just to a lesser degree than trout.

Despite the possibility of easy trout access to the reaches downstream of the abstraction intake on Limestone Creek via a connection to the Hinds River (a higher-order river downstream), trout were completely absent in all reaches. This is likely due to trout preference for deeper pools (for refuge; Davey & Kelly, 2007) and need for habitats with enough flow to deliver drifting invertebrate or terrestrial prey (Hughes *et al.*, 2003). Additionally, trout are known to be averse to human activity and movements on the streambank (Young & Hayes, 2004), perhaps causing them to avoid areas adjacent and downstream of abstraction intakes, which have higher likelihood of human visitation (i.e., abstraction structure maintenance activity and paths allowing easy access for fishermen or hikers). In areas with more flow, trout abundance relative to native fishes increased, although native fishes were still more abundant overall at all reaches (but did not always dominate in terms of biomass). This is likely due to the propensity of trout to prey upon or out-compete native fishes, especially galaxiids, when occurring in sympatry (McIntosh *et al.*, 2010).

There is a scarcity of research on the effects of small-scale abstractions and diversions on patterns of native and introduced fish co-occurrence globally, particularly for temperate fresh waters, so our findings could be particularly useful to aquatic ecosystem managers. Other studies in New Zealand also concluded that trout presence was negatively correlated with percent of water abstracted, however corresponding effects on native upland bullies or roundhead galaxias (*Galaxias anomalus*) were quite different (Leprieur *et al.*, 2006; Lange *et al.*, 2014). This supports our contention that loss of flow from abstractions may be detrimental

to large-bodied fishes (i.e., trout) and offer some relief to native taxa (i.e., bullies and galaxiids) by offsetting effects of non-natives. Many studies report native fishes suffer in relation to introduced taxa because flow modifications cause more benign habitats for invaders and poorly fit the ecological adaptations of native fish (Merciai *et al.*, 2018), but in the case of our study, the non-native species was more sensitive to anthropogenic habitat alterations than native fishes, leading to a contrasting result. There are other rare instances, similar to our findings, where flow modifications have been found to benefit native taxa (e.g., dam blocking spread of introduced trout; Lintermans, 2000). The increase in relative abundance of native fish downstream of surface-water abstractions, associated with higher flow loss, could be attributed to the flexible life-history patterns of New Zealand fish species that have developed as a response to highly variable and unpredictable flow regimes (Winterbourn, Rounick & Cowie, 1981; Lake *et al.*, 1985), enabling these taxa to cope with unpredictable flow changes associated with human demand around water abstraction sites, unlike non-native trout species (Jowett & Biggs, 2009). While native fish were able to persist in these highly-impacted locations, we have no evidence for how negatively affected the long-term health and viability of these populations are by the flow loss, for example through reduced survival or recruitment, and increased vulnerability to natural flow extremes compounding anthropogenic drying effects.

Effects on food-web characteristics

Following our expectations from *H3*, abstractions affected food-chain lengths downstream of abstraction points, although there was no associated modulation of carbon range of fish diets, which suggests there was no change in trophic breadth, but trophic height was reduced. The decrease in food-chain length with loss-of-flow below abstractions may be partially explained by the disappearance of larger-bodied fishes, which typically have higher trophic positions (*K.*

Fraley 2017 unpublished data; Arim *et al.*, 2010; thus reducing the number of trophic links in the food web). A positive association between habitat size and food-chain length has been documented across a wide range of ecosystems (Sabo *et al.*, 2010), and alterations in trophic height have often been driven by changes in the abundance or presence of large top predators (McHugh *et al.*, 2014), such as we found. The lack of response in carbon range suggests that changes in food-chain length are more substantial than changes in trophic breadth for freshwater food webs, implying that the resource base is not changing with abstraction flow loss, but trophic interactions are altered.

Contrary to expectations, we found no evidence suggesting there was an additional interaction of distance from abstraction point with decreasing local flow, or whether observations were upstream or downstream of the abstraction for any of our fish assemblage or food web characteristic metrics. We expected that distance from the abstraction would be more important for fish assemblages downstream where groundwater recharge would mitigate flow loss in the furthest downstream reaches. However, distance from the abstraction point was included as a variable in all our models to incorporate the spatial structure of our study design.

Implications

Many parts of the world are facing increasing demand for water for agricultural and municipal purposes and increasing modification of rivers (e.g., New Zealand's eastern coast, Western United States; Falke *et al.*, 2011; Booker, 2018), compounded by less precipitation, higher air temperatures, and shrinking groundwater tables due to anthropogenic development and climate warming (Malmqvist & Rundle, 2002; Vörösmarty *et al.*, 2010; Woodward, Perkins & Brown, 2010; Duncan, Srinivasan & McMillan, 2016). To balance economic needs and environmental concerns, water managers need to assess the ecological outcomes of providing additional environmental flows at the cost of reducing irrigation allocations (Bunn & Arthington, 2002;

Poff *et al.*, 2010; Horne *et al.*, 2017). While there is no consensus on the development of general, transferable relationships between water abstraction and ecological responses, there is evidence that greater alteration to flow regimes increases the risk of ecological change (Poff & Zimmerman, 2010). Supporting this, our results show that small-scale surface water abstractions can significantly affect fish assemblages, depending on the proportion of flow removed. Such changes should be investigated further at broader geographic and temporal scales (and in terms of multiple compounding abstractions) to better determine minimum flows and maximum allowable abstraction rates in rivers. This would aim to balance the need to preserve endangered native fish species and sensitive recreationally-valued introduced species, such as brown trout, to ensure fish assemblages and aquatic communities do not collapse as a result of water abstraction.

In light of our results showing that even small abstractions can affect fish assemblages, freshwater conservation and restoration efforts, typically occurring at local spatial scales (Wohl *et al.*, 2005), could be more effective if they were concentrated at strategic locations (e.g., abstraction points) within the catchment for greatest ecological outcome. In addition, managers of water resources need to consider the proportion of river flow abstracted as a parameter in addition to a set water volume (Benda, Miller & Barquín, 2011). The identification of biologically meaningful abstraction conditions for management or restoration would help to identify target locations for restoration or conservation (Booker, 2018).

There is some evidence from our findings, and from other studies, that suggest loss-of-flow can be beneficial to small-bodied native fishes vulnerable to trout predation and competition (Leprieur *et al.*, 2006); assuming river connectivity is retained for the benefit of migratory species (e.g., longfin eels and torrentfish). At first sight this might suggest that management incorporating existing water abstractions could facilitate areas of refuge for native fishes and

enhance co-occurrence between vulnerable native species and economically-important and recreationally valued introduced species (Chen & Olden, 2017). However, this would only be appropriate for cases where a native species or population is under threat of extirpation in a homogenous environment, because natural environmental heterogeneity (e.g., streams with flooding disturbance or water temperatures outside of trout-preferred ranges), already provides refugia for native taxa (Boddy & McIntosh, 2017; Chapter Three). Moreover, flow loss may still have detrimental effects on native fish, just less so than trout, so further investigation is required on the impacts of abstractions on native assemblages in the absence of invasive predators.

Given our findings, it is crucial to continue research in this area to produce scientifically defensible guidelines for water removal limits, the management of flow modification, and fisheries in regulated rivers (Poff & Zimmerman, 2010). This should be done at the riverscape-scale (Ward, Tockner & Schiemer, 1999), given the potential effects of multiple, compounding abstractions that are commonly installed. Finally, balancing economic interests and ecological values in river management is essential in light of impending climate warming and continuing human development worldwide (Horne *et al.*, 2017).

Table S1: Summary of habitat characteristics and fish assemblage metrics measured or calculated for four sampled water abstraction sites in Canterbury, New Zealand (averaged across 15 reaches within each stream). Discharge was measured on the day of sampling, maximum flow loss is the difference between the highest and lowest measured flow at any reach in the stream, wetted width represents the width of the flowing stream channel, and RDI (River Disturbance Index) scores the flood-proneness of the stream channel by a visual assessment of the bed and bank. See Table 1 for units and description of fish assemblage metrics.

Variable	Pudding Hill Stream	Taylors Stream	Limestone Creek	Kowai River
Discharge (m^3/s)	0.56	0.87	<0.01	0.32
Maximum flow loss (%)	85	57	58	100
Wetted width (m)	7.56	10.12	2.45	3.97
River Disturbance Index	104	97	65	116
Abundance (no./m)	41	83	124	48
Biomass (g)	564	801	156	224
Mass-abundance slope	-1.12	-1.03	-1.03	-1.07
Native–trout abundance ratio	6.79	15.54	N/A	33.63
Native–trout biomass ratio	1.34	5.56	N/A	4.19
Food-chain length	3.39	3.56	3.42	2.55
Carbon range	3.58	4	2.88	2.66
Maximum species diversity	3	5	2	4

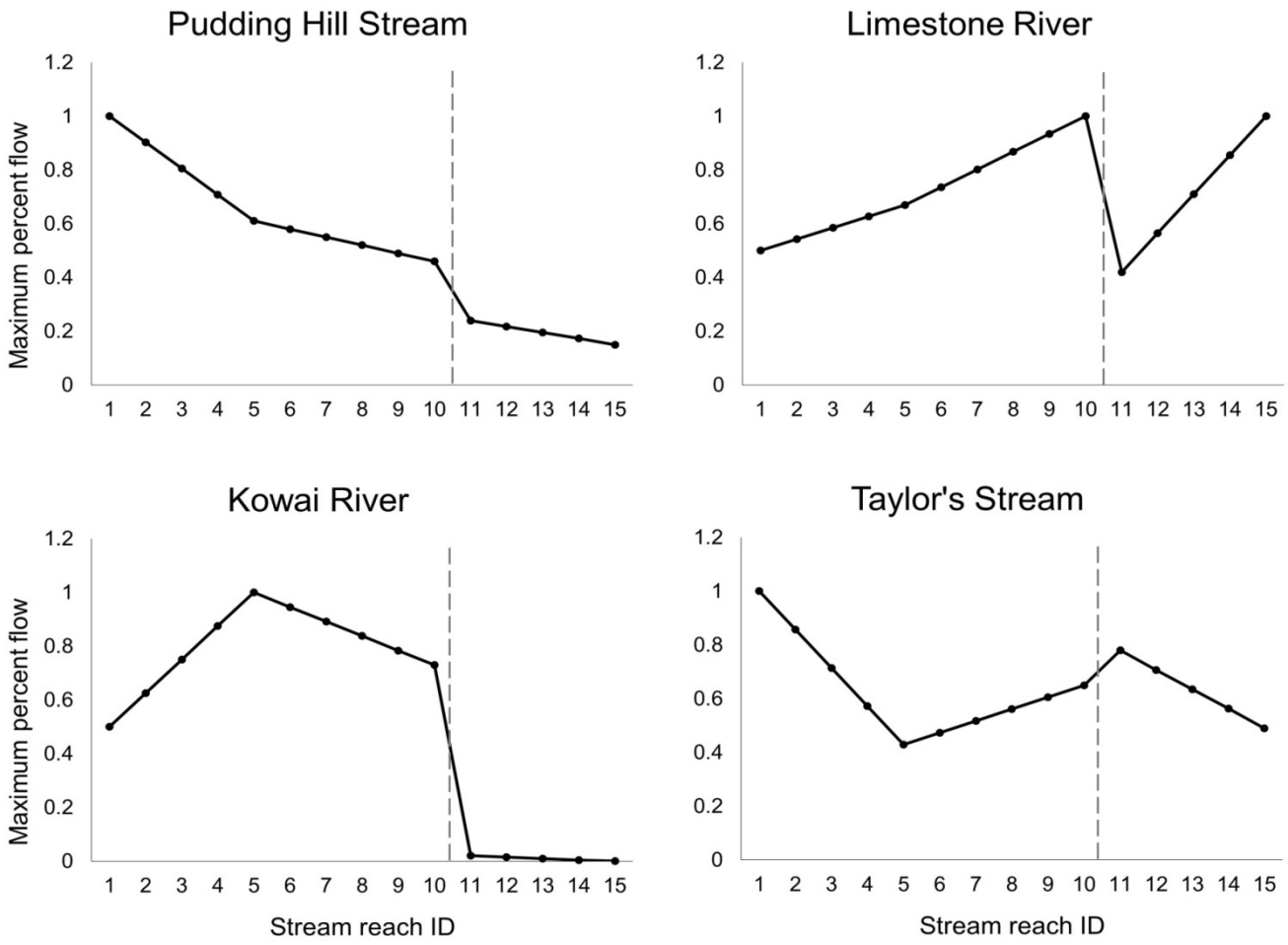

Fig. S1: Proportion of maximum stream flow for longitudinal sampling reaches around a surface water abstraction point. Reaches 1–10 were upstream of the abstraction and 11–15 were downstream. Values for reaches 2-4, 6-9, and 12-14 for all sites are interpolated discharge. The dashed vertical line denotes the abstraction point.

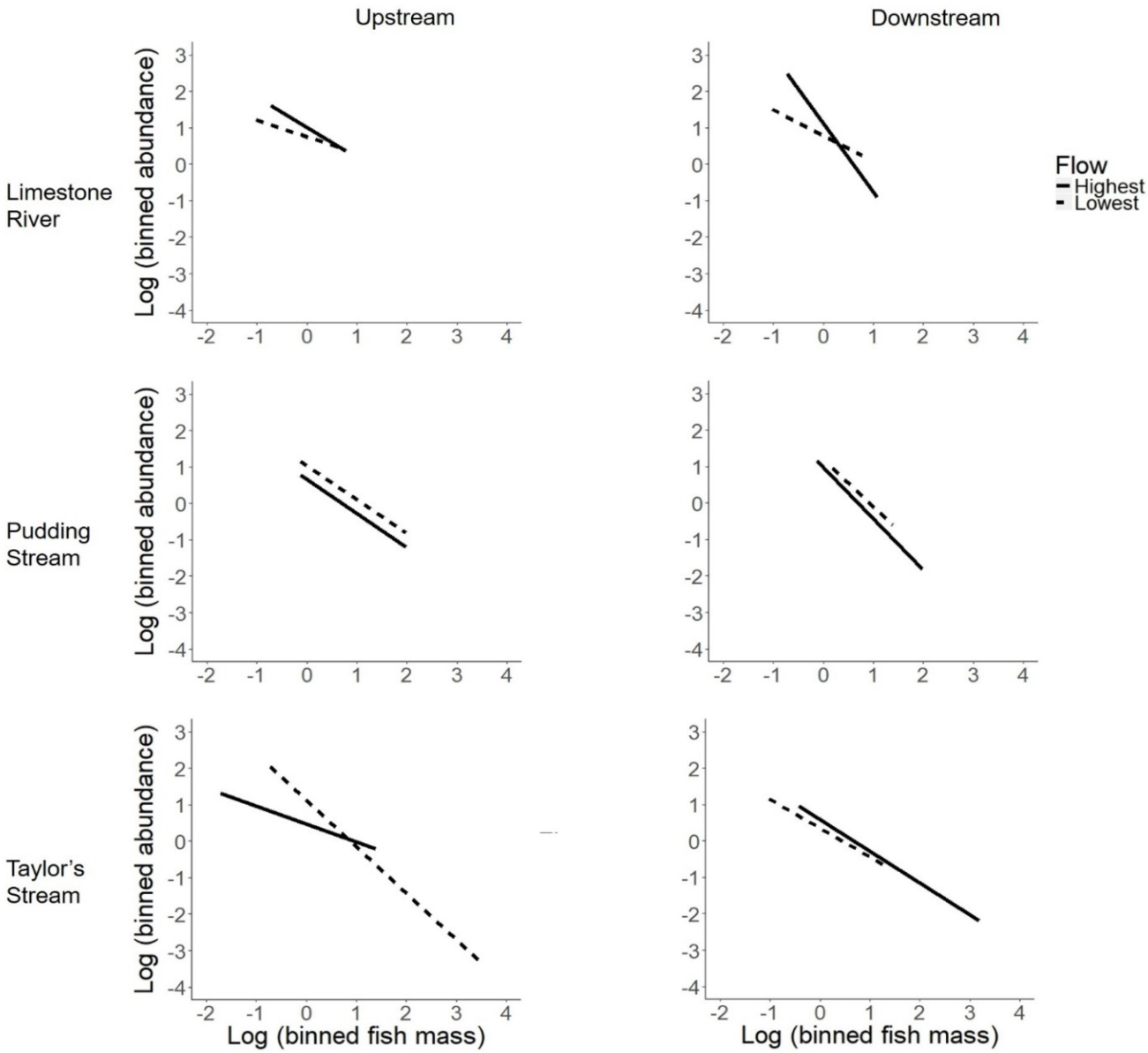

Fig. S2: Mass-abundance relationships for stream reaches with the lowest (dashed lines) and highest (solid lines) proportion of maximum flow upstream (left-hand panels) and downstream (right-hand panels) of surface water abstraction sites with sufficient data (Kowai River excluded due to reaches with zero flow). Note the addition of a larger size class of fishes (line extends further to the right) for the downstream reaches with highest flow.

Plate 5. Surface water takes sampled in the Canterbury Plains with (bottom) and without (top) a dam at the point of diversion.

Photos: Nixie Boddy

Chapter Six:

Discussion

Freshwater ecosystems are among the most threatened in the world, in part due to landscape-scale homogenisation (MEA, 2005; Dudgeon *et al.*, 2006; Zeni & Casatti, 2014), so understanding the value of habitat heterogeneity in freshwater systems is critical. Ecologically meaningful breaks in habitat type, or discontinuities, can occur both naturally (e.g. river confluences) and anthropogenically (e.g. dams and water diversions), and are likely major contributors to large-scale heterogeneity in river systems (Benda *et al.*, 2004; Kiffney *et al.*, 2006; Kennedy *et al.*, 2016). However, the consequences of the spatial juxtaposition of abiotically distinct habitat patches have rarely been considered.

Riverscapes differ from other ecological networks in that habitat can consist of both network branches and nodes, so the spatial arrangement of differing habitat patches in a river network could influence the distribution and abundance of mobile organisms, and interspecific interactions (Campbell Grant, Lowe & Fagan, 2007). With this research I focussed on how spatial heterogeneity in river flow characteristics associated with confluences and surface water diversions influenced fish assemblages. Specifically, I investigated how spatial and temporal patterns in fish assemblage structure and abundance, and the relative abundance of native and invasive fish, were influenced by discontinuities in river networks.

My results indicate that around both confluences and surface water diversions, the configuration of flow regimes and direction of flow play major roles in producing highly context-dependent fish assemblage structure and abundance, and can influence the outcome of native–invasive species interactions. I have shown that spatial heterogeneity associated with confluences and abstractions influences fish assemblage composition at larger scales

independently of currently acknowledged mechanisms such as stream order and spatial position in the catchment. In this chapter I summarise key results and illustrate how each extends current knowledge of spatial dynamics in river networks, and highlight how my results could be used to advance identification of ecologically significant characteristics of river networks and improve the strategic management of fish, especially in invaded riverscapes.

Spatial heterogeneity

Firstly, an important finding was that only some confluences cause measureable changes in biotic communities, reflecting the complex nature of tributary-mainstem interactions in an inherently spatially and temporally variable environment (Jones & Schmidt, 2017; Rice, 2017). Therefore, it is essential to develop methods to identify where these ecologically significant confluences are likely to occur. Previously, ecologically 'significant' confluences have been related to either their spatial position in the network, or to their confluence symmetry ratio, i.e., the relative size of the tributary river compared to the mainstem (Kiffney *et al.*, 2006; Milesi & Melo, 2014; Jones & Schmidt, 2017). However, the 'heterogeneity' of confluences, that is the arrangement of abiotically similar or different streams around a confluence, was poorly understood (Kiffney *et al.*, 2006; Rice, 2017). I found the spatial layout of abiotic conditions around confluences can play an important role in determining fish community composition by influencing the presence and configuration of spatial heterogeneity.

Heterogeneity caused by flood-disturbance regimes around confluences can influence fish assemblage structure and abundance (Chapters Two, Three & Four), so identification of likely locations for the juxtaposition of contrasting disturbance regimes is important for understanding large-scale spatial dynamics in fish communities. Headwater streams, for example, are predicted to more commonly have contrasting environmental conditions because they originate from smaller, more geographically specific drainage areas (Jones & Schmidt,

2017). The juxtaposition of contrasting flood disturbance regimes can support higher fish densities (Chapter Four), potentially through processes such as habitat complementation, source–sink population dynamics, resource subsidies and dispersal connectivity (Fausch *et al.*, 2002; Kiffney *et al.*, 2006; Campbell Grant, Lowe & Fagan, 2007; Rice, 2017). Therefore, given that numerous potentially community-shaping ecological processes operate at landscape scales, understanding large-scale metacommunity dynamics in spatially heterogeneous riverscapes is crucial.

Spatial heterogeneity and metapopulation dynamics

Advancing research in metapopulation dynamics and landscape ecology (Leibold *et al.*, 2004; Heino *et al.*, 2015; Dala-Corte, Becker & Melo, 2017) emphasises the need for a broader approach to stream fish ecology that considers the responses of fish to habitat heterogeneity at larger spatial and temporal scales (Fausch *et al.*, 2002). Examining spatial patterns in stream fish assemblages through the lens of patch dynamics and metacommunities allows the spatial structure of the environment and dispersal between habitat types to be accounted for. This is important because often the spatial context can be as influential as local habitat conditions in determining the richness and composition of assemblages (Bennett, Radford & Haslem, 2006). Discontinuities such as confluences and water abstractions in river networks can create spatially connected yet abrupt changes in abiotic characteristics, which create complex spatial patterns in stream fish communities likely best explained by metacommunity and patch dynamics theory (Jones & Schmidt, 2017). Metacommunity models suggest population size and large-scale species persistence in suboptimal or sink habitats can be supported by dispersal (Hanski, 1999; Dala-Corte, Becker & Melo, 2017), therefore it is possible that spatial heterogeneity could increase temporal stability by increasing potential for recolonisation or source–sink dynamics (Brown *et al.*, 2011). My results from Chapters Two and Four suggest

dispersal between spatially juxtaposed stable and disturbed stream branch habitats may be facilitating the increased fish abundance, assemblage evenness and temporal stability in native–invasive relative abundance associated with spatial heterogeneity around confluences. In Chapter Three, the relative abundance of native and invasive fish was influenced by both confluence configuration and distance to confluence, suggesting directional flow meant dispersal and recolonisation effects were more easily propagated downstream than upstream. In addition, species interactions could also limit the direction and distance that individuals can disperse from source populations (Ganio, Torgersen & Gresswell, 2005). Native galaxiids can persist in sink habitats near sources where propagule pressure is high, such as I found near heterogeneous confluences in Chapter Three, but because propagule pressure decreases with increasing distance to the source (Woodford & McIntosh, 2011), proximity to source populations could likely be driving observed spatial patterns in co-occurrence in invaded riverscapes (Chapter Three). Therefore, spatial heterogeneity associated with certain confluence configurations likely creates opportunities for directionally-biased and distance-limited source–sink and recolonisation dynamics. Thus, metacommunity processes such as dispersal and source–sink dynamics likely play a strong role in determining fish abundance and assemblage composition in heterogeneous riverscapes.

Differences in dispersal dynamics in heterogeneous versus homogenous river systems are also likely to influence temporal stability in fish assemblages. It has been suggested that temporal stability in fish populations will be greater in large mainstems than more isolated headwater streams due to centrality in the dispersal network (Dala-Corte, Becker & Melo, 2017). The results of my research, however, point to greater roles for landscape composition and configuration in driving the temporal stability of biotic assemblages and outcomes of interspecific interactions (Chapter Four). Spatially variable interspecific interactions and population-specific responses to disturbance heterogeneity may determine temporal stability in

fish assemblages at large spatial scales (Wilcox *et al.*, 2017; Chapter 4). Given how common negative interactions between native and invasive species are globally (Vitousek *et al.*, 1996; Clavero & Garcı´a-Berthou, 2005; Maciel & Lutscher, 2018), it is important to understand how disturbance heterogeneity and invasive species interact to influence native species assemblages in invaded riverscapes.

Spatial heterogeneity and invasion processes

Non-native brown and rainbow trout are more vulnerable to both floods and low flow events than native fish in New Zealand (Jowett & Richardson, 1989; Jowett, 1990; Leprieur *et al.*, 2006; Jellyman *et al.*, 2017). Invasive species abundance often drives their impact on native species (Kumschick *et al.*, 2015; Latzka *et al.*, 2016), so by limiting densities of large piscivorous trout, flow disturbance likely benefits native galaxiids, resulting in higher relative abundances. Therefore, spatial heterogeneity in flow disturbance, either naturally around confluences or anthropogenically around surface water abstractions, could mediate the strength of native–invasive interactions in these riverscapes (Chapters Three & Five). Consequently, my results highlight the role of spatial heterogeneity in disturbance regime in influencing the outcome of native–invasive species interactions at large spatial scales.

Implications for management and conservation

Knowledge of how spatial habitat mosaics influence biotic communities could facilitate management aimed at manipulating the mosaic structure to achieve certain conservation goals (Bennett, Radford & Haslem, 2006). Moreover, understanding how fish assemblages in invaded riverscapes respond to spatial heterogeneity in flow disturbance associated with confluences and surface water abstractions provides an opportunity to strategically prioritize management efforts at large spatial scales to minimise invasive species impacts (Hansen *et al.*,

2013; Vander Zanden, Hansen & Latzka, 2017). Given that funding for invasive species management generally pales in comparison to the scale of the problem, cost-effective solutions such as this that can be applied at large spatial scales are extremely valuable (Latzka *et al.*, 2016), and will likely improve ecological outcomes beyond what can be achieved with smaller-scale restoration approaches.

The lack of improvement in stream health in most restoration efforts is likely a result of reliance on reach-scale approaches due to a scarcity of large-scale solutions, therefore consideration of the spatial context of potential restoration sites within river networks, for example with regards to disturbance heterogeneity within the river networks as my results suggest, could produce more effective biological outcomes (Palmer, Menninger & Bernhardt, 2010; Brown *et al.*, 2011). Catchment-orientated conservation and management could enable strategic restoration of ecologically significant locations in river networks, such as confluences or surface water abstractions, for desired ecological outcomes (Benda, Miller & Barquín, 2011). For example, if co-existence between flood-adapted native fish and flood-vulnerable invasive species was desired, restoration could prioritize confluences between stable and flood-disturbed streams within the river network (Chapters Three & Four). Not only can catchment-scale management significantly improve stream health (Palmer, Menninger & Bernhardt, 2010), but management targeting specific spatial arrangements of flow disturbance, using network-based custom-flow design to facilitate desired biological outcomes (Chen & Olden, 2017), enables highly customisable and targeted large-scale management of riverscapes. For example, this approach could target coexistence between economically valuable invasive fish and threatened native fish, because balancing economic interests and ecological values such as these in river management is essential in light of impending climate warming and continuing human development worldwide (Horne *et al.*, 2017).

Opportunities for future development

Despite biological invasions generally occurring over large spatial scales in heterogeneous environments, the scale of resource management, most research has focussed on local or site-level impacts (Vander Zanden, Hansen & Latzka, 2017; Heasley, Clifford & Millington, 2018). I have highlighted the importance of considering larger-scale spatial heterogeneity for native–invasive dynamics in river networks (Chapters Three, Four & Five), but more research is required to untangle native–invasive coexistence from co-occurrence in invaded riverscapes. The difference between coexistence and co-occurrence of native and invasive species is crucial for river restoration and management, but is currently poorly understood in the context of large-scale spatial heterogeneity. In addition, further research on the influence of flow loss associated with surface water diversions on native fish in non-invaded river networks is required to establish whether the abundance of native fish is increased downstream due to predation-release or is flow-related.

Further investigation into mechanisms driving spatial and temporal structuring of fish assemblages in invaded riverscapes is required to reveal species-specific responses to disturbance heterogeneity. In addition, future research could investigate how spatial heterogeneity in flow regimes around confluences and abstractions influences long term population health and viability, such as temporal patterns of recruitment and survival. This is very important because it could decrease the vulnerability of fish populations to greater flow extremes, such as those associated with predicted climate change and increased pressure on water resources.

In conclusion, my research has contributed to our understanding of the complex spatial patterns in fish assemblage abundance and composition in river networks by identifying the importance of the presence and configuration of spatial heterogeneity in flow disturbance regimes, both

associated with confluences and surface water abstractions. My results also highlight the role of spatial heterogeneity in mediating the outcome of native–invasive species interactions in invaded river networks. I hope that these concepts will be further developed and implemented to provide strategic management of key network locations to assist in the preservation of threatened native species in the face of increasing invasion, intensified anthropogenic demand for water and climate change.

Plate 6. Single upstream pass electrofishing without stopnets in the Canterbury High Country.

Photos: Nixie Boddy

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hope that when I die someone will
RICHARDS

References

Anderson E.P., Freeman M.C. & Pringle C.M. (2006) Ecological consequences of hydropower development in Central America: impacts of small dams and water diversion on neotropical stream fish assemblages. *River Research and Applications,* **22,** 397-411.

Anderson R.P. (2017) When and how should biotic interactions be considered in models of species niches and distributions? *Journal of Biogeography,* **44,** 8-17.

Arim M., Abades S.R., Laufer G., Loureiro M. & Marquet P.A. (2010) Food web structure and body size: trophic position and resource acquisition. *Oikos,* **119,** 147-153.

Baltz D.M. & Moyle P.B. (1984) Segregation by species and size classes of rainbow trout, *Salmo gairdneri*, and Sacramento sucker, *Catostomus occidentalis,* in three California streams. *Environmental Biology of Fishes,* **10,** 101-110.

Barton K. (2016) MuMIn: multi-model inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn.

Basse B. & McLennan J.A. (2003) Protected areas for kiwi in mainland forests of New Zealand: how large should they be. *New Zealand Journal of Ecology,* **27,** 95-105.

Bates D., Maechler M., Bolker B. & Walker S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software,* **67,** 1-48.

Bellmore J.R., Baxter C.V. & Connolly P.J. (2015) Spatial complexity reduces interaction strengths in the meta-food web of a river floodplain mosaic. *Ecology,* **96,** 274-283.

Benda L., Miller D. & Barquín J. (2011) Creating a catchment scale perspective for river restoration. *Hydrology and Earth System Sciences,* **15,** 2995-3015.

Benda L., Poff N.L., Miller D., Dunne T., Reeves G.H., Pess G. & Pollock M. (2004) The network dynamics hypothesis: how channel networks structure riverine habitats. *BioScience,* **54,** 413-427.

Bennett A.F., Radford J.Q. & Haslem A. (2006) Properties of land mosaics: implications for nature conservation in agricultural environments. *Biological Conservation,* **133,** 250-264.

Benstead J.P., March J.G., Pringle C.M. & Scatena F.N. (1999) Effects of low-head dam and water abstraction on migratory tropical stream biota. *Ecological Applications,* **9,** 656-668.

Boddy N.C. & McIntosh A.R. (2017) Temperature, invaders and patchy habitat interact to limit the distribution of a vulnerable freshwater fish. *Austral Ecology,* **42,** 456-467.

Bonetto A.A., Wais J.R. & Castello H.P. (1989) The increasing damming of the Paraná Basin and its effect on the lower reaches. *Regulated Rivers: Research and Management,* **4,** 333-346.

Booker D.J. (2018) Quantifying the hydrological effect of permitted water abstractions across spatial scales. *Environmental Management***,** in press doi.org/10.1007/s00267-018-1040-7.

Booker D.J., Whitehead A.L., Henderson R.D. & Yang J. (2016) Nationally consistent methods for calculating water allocation indicators. National Institute of Water & Atmospheric Research report to Ministry for the Environment, Christchurch, New Zealand.

Bosem Baillod A., Tscharntke T., Clough Y., Batáry P. & Marini L. (2017) Landscape-scale interactions of spatial and temporal cropland heterogeneity drive biological control of cereal aphids. *Journal of Applied Ecology,* **54,** 1804-1813.

Brewitt K.S., Danner E.M. & Moore J.W. (2017) Hot eats and cool creeks: juvenile Pacific salmonids use mainstem prey while in thermal refuges. *Canadian Journal of Fisheries and Aquatic Sciences,* **74**, 1588-1602.

Brose U., Martinez N.D. & Williams R.J. (2003) Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology,* **84,** 2364-2377.

Brown B.L. (2007) Habitat heterogeneity and disturbance influence patterns of community temporal variability in a small temperate stream. *Hydrobiologia,* **586,** 93-106.

Brown B.L., Swan C.M., Auerbach D.A., Campbell Grant E.H., Hitt N.P., Maloney K.O. & Patrick C. (2011) Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. *Journal of the North American Benthological Society,* **30,** 310-327.

Brown L.E., Hannah D.M. & Milner A.M. (2007) Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. *Global Change Biology,* **13,** 958-966.

Brunke M. & Gonser T.O.M. (1997) The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology,* **37,** 1-33.

Budy P., Thiede G.P., McHugh P., Hansen E.S. & Wood J. (2008) Exploring the relative influence of biotic interactions and environmental conditions on the abundance and distribution of exotic brown trout (*Salmo trutta*) in a high mountain stream. *Ecology of Freshwater Fish,* **17,** 554-566.

Bunn S.E. & Arthington A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management,* **30,** 492-507.

Campbell Grant E.H., Lowe W.H. & Fagan W.F. (2007) Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters,* **10,** 165-175.

Campbell R.E. & McIntosh A.R. (2017) Space-time interactions and invertebrate assemblage change in stream networks. *Austral Ecology,* **42,** 227-237.

Cantrell R., Cosner C. & Lou Y. (2007) Advection-mediated coexistence of competing species. *Proceedings of the Royal Society of Edinburgh Section A,* **137,** 497-518.

Caswell H. & Cohen J.E. (1991) *Communities in patchy environments: a model of disturbance, competition, and heterogeneity,* Springer-Verlag, New York.

Cathcart C.N., Gido K.B., McKinstry M.C. & MacKinnon P.D. (2018) Patterns of fish movement at a desert river confluence. *Ecology of Freshwater Fish,* **27,** 492-505.

Chamberlain S.A., Bronstein J.L. & Rudgers J.A. (2014) How context dependent are species interactions? *Ecology Letters,* **17,** 881-890.

Chase J.M., Biro E.G., Ryberg W.A. & Smith K.G. (2009) Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities. *Ecology Letters,* **12,** 1-9.

Chen W. & Olden J.D. (2017) Designing flows to resolve human and environmental water needs in a dam-regulated river. *Nature Communications,* **8,** 2158.

Chisholm C., Lindo Z. & Gonzalez A. (2011) Metacommunity diversity depends on connectivity and patch arrangement in heterogeneous habitat networks. *Ecography,* **34,** 415-424.

Clavero M. & Garcı´a-Berthou E. (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution,* **20,** 110-110.

Cromsigt J.P.G.M., Prins H.H.T. & Olff H. (2009) Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. *Diversity and Distributions,* **15,** 513-522.

Czeglédi I., Sály P., Takács P., Dolezsai A., Nagy S.A. & Erős T. (2015) The scales of variability of stream fish assemblages at tributary confluences. *Aquatic Sciences,* **78,** 641-654.

Dala-Corte R.B., Becker F.G. & Melo A.S. (2017) The importance of metacommunity processes for long-term turnover of riffle-dwelling fish assemblages depends on spatial position within a dendritic network. *Canadian Journal of Fisheries and Aquatic Sciences,* **74,** 101-115.

Datry T., Arscott D. & Sabater S. (2011) Recent perspectives on temporary river ecology. *Aquatic Sciences - Research Across Boundaries,* **73,** 453-457.

Dauwalter D.C. & Pert E.J. (2003) Effect of electrofishing effort on an index of biotic integrity. *North American Journal of Fisheries Management,* **23,** 1247-1252.

Davey A.J.H., Kelly D.J. & Biggs B.J.F. (2006) Refuge use strategies of stream fishes in response to extreme low flows. *Journal of Fish Biology,* **69,** 1047-1059.

Death R.G., Dewson Z.S. & James A.B. (2009) Is structure or function a better measure of the effects of water abstraction on ecosystem integrity? *Freshwater Biology,* **54,** 2037-2050.

Deitch M.J., Kondolf G.M. & Merenlender A.M. (2009) Surface water balance to evaluate the hydrological impacts of small instream diversions and application to the Russian River basin, California, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **19,** 274-284.

Dewson Z.S., James A.B. & Death R.G. (2007a) Invertebrate responses to short-term water abstraction in small New Zealand streams. *Freshwater Biology,* **52,** 357-369.

Dewson Z.S., James A.B. & Death R.G. (2007b) A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society,* **26,** 401-415.

Donohue I., Hillebrand H., Montoya J.M., Petchey O.L., Pimm S.L., Fowler M.S., Healy K., Jackson A.L., Lurgi M., McClean D., O'Connor N.E., O'Gorman E.J. & Yang Q. (2016) Navigating the complexity of ecological stability. *Ecology Letters,* **19,** 1172-1185.

Dormann C.F., McPherson J.M., Araújo M.B., Bivand R., Bolliger J., Carl G., Davies R.G., Hirzel A., Jetz W., Kissling W.D., Kühn I., Ohlemüller R., Peres-Neto P., Reineking B., Schröder B., Schurr F.M. & Wilson R. (2007) Methods to account for spatial

autocorrelation in the analysis of species distributional data: a review. *Ecography,* **30,** 609-628.

Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z., Knowler D.J., Leveque C., Naiman R.J., Prieur-Richard A.H., Soto D., Stiassny M.L. & Sullivan C.A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society,* **81,** 163-182.

Duncan M.J., Srinivasan M.S. & McMillan H. (2016) Field measurement of groundwater recharge under irrigation in Canterbury, New Zealand, using drainage lysimeters. *Agricultural Water Management,* **166,** 17-32.

Dynesius M. & Nilsson C. (1994) Fragmentation and flow regulation or river systems in the northern third of the world. *Science,* **266,** 753-762.

Falke J.A., Fausch K.D., Magelky R., Aldred A., Durnford D.S., Riley L.K. & Oad R. (2011) The role of groundwater pumping and drought in shaping ecological futures for stream fishes in a dryland river basin of the western Great Plains, USA. *Ecohydrology,* **4,** 682-697.

Faraway J.J. (2016) *Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models, second edition.*, CRC press, Boca Raton.

Fausch K.D. (1988) Tests of competition between native and introduced salmonids in streams: what have we learned? *Canadian Journal of Fisheries and Aquatic Sciences,* **45,** 2238-2246.

Fausch K.D., Tanguchi Y., Nakano S., Grossman G.D. & Townsend C.R. (2001) Flood disturbance regimes influence rainbow trout invasion success among five holoarctic regions. *Ecological Applications,* **11,** 1438-1455.

Fausch K.D., Torgersen C.E., Baxter C.V. & Li H.W. (2002) Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience,* **52,** 483-498.

Fernandes C.C., Podos J. & Lundberg J.G. (2004) Amazonian ecology: tributaries enhance the diversity of electric fishes. *Science,* **305,** 1960-1962.

Ficetola G.F. & De Bernardi F. (2005) Supplementation or *in situ* conservation? Evidence of local adaptation in the Italian agile frog *Rana latastei* and consequences for the management of populations. *Animal Conservation,* **8,** 33-40.

Flitcroft R.L., Burnett K.M., Reeves G.H. & Ganio L.M. (2012) Do network relationships matter? Comparing network and instream habitat variables to explain densities of juvenile coho salmon (*Oncorhynchus kisutch*) in mid-coastal Oregon, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **22,** 288-302.

Fox J. (2003) Effect Displays in R for Generalised Linear Models. *Journal of Statistical Software,* **8,** 1-27.

Fraley K.M., Warburton H.J., Jellyman P.G., Kelly D. & A.R. M. (2018) Responsiveness of fish mass–abundance relationships and trophic metrics to flood disturbance, stream size, land cover and predator taxa presence in headwater streams. *Ecology of Freshwater Fish***,** In press. https://doi.org/10.1111/eff.12410.

Fraterrigo J.M. & Rusak J.A. (2008) Disturbance-driven changes in the variability of ecological patterns and processes. *Ecology Letters,* **11,** 756-770.

Ganio L.M., Torgersen C.E. & Gresswell R.E. (2005) A geostatistical approach for describing spatial pattern in stream networks. *Frontiers in Ecology and the Environment,* **3,** 138-144.

Garcia X.F., Schnauder I. & Pusch M.T. (2012) Complex hydromorphology of meanders can support benthic invertebrate diversity in rivers. *Hydrobiologia,* **685,** 49-68.

Goodman J.M., Dunn N., Ravenscroft P., Allibone R.M., Boubee J.A.T., David B.O., Griffiths M., Ling N., Hitchmough R. & Rolfe J.R. (2014) Conservation status of New Zealand freshwater fish, 2013. In: *New Zealand Threat Classification Series 7.* (Ed L. Clelland), p. 12. Department of Conservation, Wellington, New Zealand, Publishing Team, Department of Conservation, PO Box 10420, The Terrace, Wellington 6143, New Zealand.

Gravel D., Massol F. & Leibold M.A. (2016) Stability and complexity in model meta-ecosystems. *Nature Communications,* **7,** 12457.

Green J.C. (2003) The precision of sampling grain size percentiles using the Wolman method. *Earth Surface Processes and Landforms,* **28,** 979-991.

Grenouillet G., Pont D. & Herisse C. (2004) Within-basin fish assemblage structure: the relative influence of habitat versus stream spatial position on local species richness. *Canadian Journal of Fisheries and Aquatic Sciences,* **61,** 93-102.

Grimm V. & Wissel C. (1997) Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia,* **109,** 323-334.

Grossman G.D., Ratjczak R.E., Crawford M. & Freeman M.C. (1998) Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecological Monographs,* **68,** 396-420.

Habit E., Piedra P., Ruzzante D.E., Walde S.J., Belk M.C., Cussac V.E., Gonzalez J. & Colin N. (2010) Changes in the distribution of native fishes in response to introduced species and other anthropogenic effects. *Global Ecology and Biogeography,* **19,** 697-710.

Hanisch J.R., Tonn W.M., Paszkowski C.A. & Scrimgeour J.G. (2010) δ13C and δ15N signatures in muscle and fin tissues: nonlethal sampling methods for stable isotope analysis of salmonids. *North American Journal of Fisheries Management*, **30,** 1-11.

Hansen G.J., Vander Zanden M.J., Blum M.J., Clayton M.K., Hain E.F., Hauxwell J., Izzo M., Kornis M.S., McIntyre P.B., Mikulyuk A., Nilsson E., Olden J.D., Papes M. & Sharma S. (2013) Commonly rare and rarely common: comparing population abundance of invasive and native aquatic species. *PLOS One,* **8,** e77415.

Hanski I. (1999) *Metapopulation ecology,* Oxford University Press., Oxford, UK, and New York, NY.

Harris J.H. (1984) Impoundment of coastal drainages of south-eastern Australia, and a review of its relevance to fish migrations. *Australian Zoologist,* **21,** 235-250.

Hart D.D. & Finelli C.M. (1999) Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics,* **30,** 363-395.

Hasegawa K., Mori T. & Yamazaki C. (2016) Density-dependent effects of non-native brown trout *Salmo trutta* on the species-area relationship in stream fish assemblages. *Journal of Fish Biology*, **90,** 370-383.

Haxton T.J. & Findlay C.S. (2008) Meta-analysis of the impacts of water management on aquatic communities. *Canadian Journal of Fisheries and Aquatic Sciences,* **65,** 437-447.

Heasley E.L., Clifford N.J. & Millington J.D.A. (2018) Integrating network topology metrics into studies of catchment-level effects on habitat diversity. *Hydrology and Earth System Sciences Discussions***,** in press doi.org/10.5194/hess-2018-89.

Heino J., Melo A.S., Siqueira T., Soininen J., Valanko S. & Bini L.M. (2015) Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology,* **60,** 845-869.

Hitt N.P. & Angermeier P.L. (2008) Evidence for fish dispersal from spatial analysis of stream network topology. *Journal of the North American Benthological Society*, **27,** 304-320.

Horne A., Webb A., Stewardson M., Richter B. & Acreman M.E. (2017) *Water for the environment: from policy and science to implementation and management*, Academic Press, Cambridge, Massachusetts.

Hovick T.J., Elmore R.D., Fuhlendorf S.D., Engle D.M. & Hamilton R.G. (2016) Spatial heterogeneity increases diversity and stability in grassland bird communities. *Ecological Applications,* **25,** 662-672.

Hughes N.F., Hayes J.W., Shearer K.A. & Young R.G. (2003) Testing a model of drift-feeding using three-dimensional videography of wild brown trout, *Salmo trutta*, in a New Zealand river. *Canadian Journal of Fisheries and Aquatic Sciences,* **60,** 1462-1476.

Iwasaki A. & Noda T. (2018) A framework for quantifying the relationship between intensity and severity of impact of disturbance across types of events and species. *Scientific Reports,* in press doi.org/10.1038/s41598-017-19048-5.

Jackson D.A., Peres-Neto P. & Olden J.D. (2001) What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences,* **58,** 157-170.

Jellyman P.G., Booker D.J., Crow S.K., Bonnett M.L. & Jellyman D. (2013) Does one size fit all? An evaluation of length-weight relationships for New Zealand's freshwater fish species. *New Zealand Journal of Marine and Freshwater Research,* **47,** 450-468.

Jellyman P.G., Booker D.J. & McIntosh A.R. (2013) Quantifying the direct and indirect effects of flow-related disturbance on stream fish assemblages. *Freshwater Biology*, **58,** 2614-2631.

Jellyman P.G., McHugh P.A., Simon K.S., Thompson R.M. & McIntosh A.R. (2017) The effects of brown trout on the trophic webs of New Zealand streams. In: *Brown trout: biology, ecology and management.* (Eds J. Lobón-Cerviá & N. Sanz), pp. 570-597. John Wiley & Sons Ltd, Hoboken, New Jersey.

Jellyman P.G. & McIntosh A.R. (2010) Recruitment variation in a stream galaxiid fish: multiple influences on fry dynamics in a heterogeneous environment. *Freshwater Biology,* **55,** 1930-1944.

Jennings S., Greenstreet S., Hill L., Piet G., Pinnegar J. & Warr K.J. (2002) Long-term trends in the trophic structure of the North Sea fish community: evidence from stable-isotope analysis, size-spectra and community metrics. *Marine Biology,* **141,** 1085-1097.

Jones N.E. & Schmidt B.J. (2017) Tributary effects in rivers: interactions of spatial scale, network structure, and landscape characteristics. *Canadian Journal of Fisheries and Aquatic Sciences,* **74,** 503-510.

Jones P.E. & Closs G.P. (2015) Life history influences the vulnerability of New Zealand galaxiids to invasive salmonids. *Freshwater Biology,* **60,** 2127-2141.

Jowett I.G. (1990) Factors related to the distribution and abundance of brown and rainbow trout in New Zealand clear-water rivers. *New Zealand Journal of Marine and Freshwater Research,* **24,** 429-440.

Jowett I.G. & Biggs B.J. (2009) Application of the 'natural flow paradigm' in a New Zealand context. *River Research and Applications,* **25,** 1126-1135.

Jowett I.G. & Richardson J. (1989) Effects of a severe flood on instream habitat and trout populations in seven New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research,* **23,** 11-17.

Joy M.K. & Death R.G. (2001) Control of fish and crayfish community structure in Taranaki, New Zealand: dams, diadromy or habitat structure. *Freshwater Biology,* **46,** 417-429.

Kennedy C.G., Mather M.E., Smith J.M., Finn J.T. & Deegan L.A. (2016) Discontinuities concentrate mobile predators: quantifying organism-environment interactions at a seascape scale. *Ecosphere,* **7,** e01226.

Kiffney P.M., Greene C.M., Hall J.E. & Davies J.R. (2006) Tributary streams create spatial discontinuities in habitat, biological productivity, and diversity in mainstem rivers. *Canadian Journal of Fisheries and Aquatic Sciences,* **63,** 2518-2530.

Kumschick S., Gaertner M., Vilà M., Essl F., Jeschke J.M., Pyšek P., Ricciardi A., Bacher S., Blackburn T.M., Dick J.T.A., Evans T., Hulme P.E., Kühn I., Mrugała A., Pergl J., Rabitsch W., Richardson D.M., Sendek A. & Winter M. (2015) Ecological impacts of alien species: quantification, scope, caveats, and recommendations. *BioScience,* **65,** 55-63.

Lake P.S. (2000) Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society,* **19,** 573-592.

Lake P.S., Barmuta L.A., Boulton A.J., Campbell I.C. & St. Clair R.M. (1985) Australian streams and Northern Hemisphere stream ecology: comparisons and problems. *Proceedings of the Ecological Society of Australia,* **14,** 61-82.

Lancaster J. & Waldron S. (2001) Stable isotope values of lotic invertebrates: sources of variation, experimental design, and statistical interpretation. *Limnology and Oceanography,* **46,** 723-730.

Lange K., Townsend C.R., Gabrielsson R., Chanut P. & Matthaei C.D. (2014) Responses of stream fish populations to farming intensity and water abstraction in an agricultural catchment. *Freshwater Biology,* **59,** 286-299.

Latzka A.W., Hansen G.J., Kornis M.S. & Vander Zanden M.J. (2016) Spatial heterogeneity in invasive species impacts at the landscape scale. *Ecosphere,* **7,** e01311.

Layman C.A., Winemiller K.O., Arrington D.A. & Jepsen D.B. (2005) Body size and trophic position in a diverse tropical food web. *Ecology,* **86,** 2530-2535.

Leathwick J.R., Elith J., Chadderton W.L., Rowe D. & Hastie T. (2008) Dispersal, disturbance and the contrasting biogeographies of New Zealand's diadromous and non-diadromous fish species. *Journal of Biogeography,* **35,** 1481-1497.

Ledger M.E., Brown L.E., Edwards F., Milner A.M. & Woodward G. (2013) Drought alters the structure and functioning of complex food webs. *Nature Climate Change,* **3,** 223-227.

Leibold M.A., Chase J.M. & Ernest S.K. (2017) Community assembly and the functioning of ecosystems: how metacommunity processes alter ecosystem attributes. *Ecology,* **98,** 909-919.

Leibold M.A., Holyoak M., Mouquet N., Amarasekare P., Chase J.M., Hoopes M.F., Holt R.D., Shurin J.B., Law R., Tilman D., Loreau M. & Gonzalez A. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters,* **7,** 601-613.

Leprieur F., Hickey M.A., Arbuckle C.J., Closs G.P., Brosse S. & Townsend C.R. (2006) Hydrological disturbance benefits a native fish at the expense of an exotic fish. *Journal of Applied Ecology,* **43,** 930-939.

Li H. & Reynolds J.F. (1995) On definition and quantification of heterogeneity. *Oikos,* **73,** 280-284.

Lintermans M. (2000) Recolonization by the mountain galaxias *Galaxias olidus* of a montane stream after the eradication of rainbow trout *Oncorhynchus mykiss*. *Marine and Freshwater Research,* **51,** 799-804.

Logue J.B., Mouquet N., Peter H., Hillebrand H. & Metacommunity Working G. (2011) Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology and Evolution,* **26,** 482-491.

Lowe S., Browne M., Boudjelas S. & De Poorter M. (2000) 100 of the world's worst invasive alien species. A selection from the Global Invasive Species Database. Invasive Species Specialist Group (ISSG), World Conservation Union (IUCN), Auckland, New Zealand.

Lundqvist J. (1998) Avert looming hydrocide. *Ambio,* **27,** 428-433.

Maciel G.A. & Lutscher F. (2018) Movement behaviour determines competitive outcome and spread rates in strongly heterogeneous landscapes. *Theoretical Ecology***,** in press doi.org/10.1007/s12080-12018-10371-12086.

Maddock I. (1999) The importance of physical habitat assessment for evaluating river health. *Freshwater Biology,* **41,** 373-391.

Magalhães M.F., Beja P., Canas C. & Collares-Pereira M.J. (2002) Functional heterogeneity of dry-season fish refugia across a Mediterranean catchment: the role of habitat and predation. *Freshwater Biology,* **47,** 1919-1934.

Malmqvist B. & Rundle S. (2002) Threats to the running water ecosystems of the world. *Environmental Conservation,* **29,** 134-153.

Matthaei C.D., Piggott J.J. & Townsend C.R. (2010) Multiple stressors in agricultural streams: interactions among sediment addition, nutrient enrichment and water abstraction. *Journal of Applied Ecology,* **47,** 639-649.

McCarthy I.D. & Waldron S. (2000) Identifying migratory *Salmo trutta* using carbon and nitrogen stable isotope ratios. *Rapid Communications in Mass Spectrometry,* **14,** 1325-1331.

McCluney K.E., Poff N.L., Palmer M.A., Thorp J.H., Poole G.C., Williams B.S., Williams M.R. & Baron J.S. (2014) Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human alterations. *Frontiers in Ecology and the Environment,* **12,** 48-58.

McDowall R.M. (2003) Impacts of introduced salmonids on native galaxiids in New Zealand upland streams: a new look at an old problem. *Transactions of the American Fisheries Society,* **132,** 229-238.

McDowall R.M. (2006) Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes? *Reviews in Fish Biology and Fisheries,* **16,** 233-422.

McDowall R.M. & Richardson J. (1983) The New Zealand freshwater fish survey, a guide to input and output., pp. 1-15. New Zealand Ministry of Agriculture and Fisheries, Fisheries Research Division Information Leaflet, Wellington, New Zealand.

McHugh P.A., McIntosh A.R., Howard S. & Budy P. (2012) Niche flexibility and trout-galaxiid co-occurrence in a hydrologically diverse riverine landscape. *Biological Invasions,* **14,** 2393-2406.

McHugh P.A., McIntosh A.R. & Jellyman P.G. (2010) Dual influences of ecosystem size and disturbance on food chain length in streams. *Ecology Letters,* **13,** 881-890.

McHugh P.A., Thompson R.M., Greig H.S., Warburton H.J. & McIntosh A.R. (2014) Habitat size influences food web structure in drying streams. *Ecography,* **38,** 700-712.

McIntosh A.R. (2000) Habitat- and size-related variations in exotic trout impacts on native galaxiid fishes in New Zealand streams. *Canadian Journal of Fisheries and Aquatic Sciences,* **57,** 2140-2151.

McIntosh A.R., Crowl T.A. & Townsend C.R. (1994) Size-related impacts of introduced brown trout on the distribution of native common river galaxias. *New Zealand Journal of Marine and Freshwater Research,* **28,** 135-144.

McIntosh A.R., McHugh P.A. & Budy P. (2012) *Salmo trutta* L. (brown trout). In: *A handbook of global freshwater invasive species.* (Ed R.A. Francis), pp. 285-296. London: Routledge.

McIntosh A.R., McHugh P.A., Dunn N., Goodman J.M., Howard S.W., Jellyman P.G., O'Brien L.K., Nyström P. & Woodford D.J. (2010) The impact of trout on galaxiid fishes in New Zealand. *New Zealand Journal of Ecology,* **34,** 195-206.

MEA. (2005) *Millennium Ecosystem Assessment. Ecosystems and human well-being: synthesis,* Island Press, Washington DC.

Merciai R., Bailey L.L., Bestgen K.R., Fausch K.D., Zamora L., Sabater S. & García-Berthou E. (2018) Water diversion reduces abundance and survival of two Mediterranean cyprinids. *Ecology of Freshwater Fish,* **27,** 481-491.

Milesi S.V. & Melo A.S. (2014) Conditional effects of aquatic insects of small tributaries on mainstream assemblages: position within drainage network matters. *Canadian Journal of Fisheries and Aquatic Sciences,* **71,** 1-9.

Moorhouse T.P. & Macdonald D.W. (2014) Are invasives worse in freshwater than terrestrial ecosystems? *Wiley Interdisciplinary Reviews: Water,* **2,** 1-8.

Morita K. (2018) Assessing the long-term causal effect of trout invasion on a native charr. *Ecological Indicators,* **87,** 189-192.

Murchie K.J., Hair K.P.E., Pullen C.E., Redpath T.D., Stephens H.R. & Cooke S.J. (2008) Fish response to modified flow regimes in regulated rivers: research methods, effects and opportunities. *River Research and Applications,* **24,** 197-217.

MykrÄ H., Heino J., Oksanen J. & Muotka T. (2011) The stability-diversity relationship in stream macroinvertebrates: influences of sampling effects and habitat complexity. *Freshwater Biology,* **56,** 1122-1132.

Naiman R.J., Magnuson J.J., McKnight D.M. & Stanford J.A. (1995) *The freshwater imperative: a research agenda,* Island Press, Washington, DC.

Nakagawa S. & Schielzeth H. (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution,* **4,** 133-142.

Nilsson C., Reidy C.A., Dynesius M. & Revenga C. (2005) Fragmentation and flow regulation of the world's large river systems. *Science,* **308,** 405-408.

Niu S.Q., Franczyk M.P. & Knouft J.H. (2012) Regional species richness, hydrological characteristics and the local species richness of assemblages of North American stream fishes. *Freshwater Biology,* **57,** 2367-2377.

Oksanen J., Blanchet F.G., Friendly M., Kindt R., Legendre P., McGlinn D., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Szoecs E. & Wagner H. (2017) Vegan: community ecology package. R package version 2.4-3. https://CRAN.R-project.org/package=vegan.

Olden J.D. (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography,* **33,** 2027-2039.

Osborne L.L. & Wiley M.J. (1992) lnfluence of tributary spatial position on the structure of warmwater fish communities. *Canadian Journal of Fisheries and Aquatic Sciences,* **49,** 671-681.

Palmer M.A., Menninger H.L. & Bernhardt E. (2010) River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice. *Freshwater Biology,* **55,** 205-222.

Papanikolaou A.D., Kühn I., Frenzel M. & Schweiger O. (2016) Landscape heterogeneity enhances stability of wild bee abundance under highly varying temperature, but not under highly varying precipitation. *Landscape Ecology,* **32,** 581-593.

Peláez O.E., Azevedo F.M. & Pavanelli C.S. (2017) Environmental heterogeneity explains species turnover but not nestedness in fish assemblages of a Neotropical basin. *Acta Limnologica Brasiliensia,* **29,** e117.

Peterson E. & Ver Hoef J.M. (2010) A mixed-model moving-average approach to geostatistical modeling in stream networks. *Ecology,* **91,** 644-651.

Petts G.E. (1984) Sedimentation within a regulated river. *Earth Surface Processes and Landforms,* **9,** 125-134.

Pfankuch D.J. (1975) Stream reach inventory and channel stability evaluation. Report of United States Department of Agriculture Forest Service, Region 1, Missoula, Montana, U.S.A.

Pickett S.T.A. & Cadenasso M.L. (1995) Landscape ecology: spatial heterogeneity in ecological systems. *Science,* **269,** 331-334.

Pittock J., Hansen L.J. & Abell R. (2008) Running dry: freshwater biodiversity, protected areas and climate change. *Biodiversity,* **9,** 30-38.

Poff N.L. & Allan J.D. (1995) Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology,* **76,** 606-627.

Poff N.L., Richter B.D., Arthington A.H., Bunn S.E., Naiman R.J., Kendy E., Acreman M., Apse C., Bledsoe B.P., Freeman M.C., Henriksen J., Jacobson R.B., Kennen J.G., Merritt D.M., O'Keeffe J.H., Olden J.D., Rogers K., Tharme R.E. & Warner A. (2010) The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards. *Freshwater Biology,* **55,** 147-170.

Poff N.L. & Zimmerman J.K.H. (2010) Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology,* **55,** 194-205.

Poisot T., Stouffer D.B. & Gravel D. (2015) Beyond species: why ecological interaction networks vary through space and time. *Oikos,* **124,** 243-251.

Post D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology,* **83,** 703-718.

Post D.M., Layman C.A., Arrington D.A., Takimoto G., Quattrochi J. & Montana C.G. (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analysis. *Oecologia,* **152,** 179-189.

Power M.E., Stewart A.J. & Matthews W.J. (1988) Grazer control of algae in an Ozark mountain stream: effects of short-term exclusion. *Ecology,* **69,** 1894-1898.

Pulliam H.R. (1988) Sources, sinks, and population regulation. *The American Naturalist,* **132,** 652-661.

Pusey B.J., Storey A.W., Davies P.M. & Edward D.H.D. (1989) Spatial and temporal variation in fish communities in two south-western Australian river systems. *Journal of the Royal Society of Western Australia,* **71,** 69-75.

R Development Core Team. (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. R Foundation for Statistical Computing. https://www.R-project.org/, Vienna, Austria.

Rice S.P. (2017) Tributary connectivity, confluence aggradation and network biodiversity. *Geomorphology,* **277,** 6-16.

Rice S.P., Greenwood M.T. & Joyce C.B. (2001) Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. *Canadian Journal of Fisheries and Aquatic Sciences,* **58,** 824-840.

Sabo J.L., Finlay J.C., Kennedy T. & Post D.M. (2010) The role of discharge variation in scaling of drainage area and food chain length in rivers. *Science,* **330,** 965-967.

Sanderson B.L., Tran C.D., Coe H.J., Pelekis V., Steel E.A. & Reichert W.L. (2009) Nonlethal sampling of fish caudal fins yields valuable stable isotope data for threatened and endangered fishes. *Transactions of the American Fisheries Society,* **138,** 1166-1177.

Sarkar D. (2008) *Lattice: multivariate data visualisation with R.* Springer, New York.

Scheiner S.M. & Willig M.R. (2008) A general theory of ecology. *Theoretical Ecology,* **1,** 21-28.

Schlosser I.J. & Kallemeyn L.W. (2000) Spatial variation in fish assemblages across a beaver-influenced successional landscape. *Ecology,* **81,** 1371-1382.

Schneck F. & Melo A.S. (2013) High assemblage persistence in heterogeneous habitats: an experimental test with stream benthic algae. *Freshwater Biology,* **58,** 365-371.

Simonson T.D. & Lyons J. (1995) Comparason of catch per unit effort and removal procedures for sampling stream fish assemblages. *North American Journal of Fisheries Management,* **15,** 419-427.

Smith J.M. & Mather M.E. (2013) Beaver dams maintain fish biodiversity by increasing habitat heterogeneity throughout a low-gradient stream network. *Freshwater Biology,* **58,** 1523-1538.

Sowersby W., Thompson R.M. & Wong B.B.M. (2015) Invasive predator influences habitat preferences in a freshwater fish. *Environmental Biology of Fishes,* **99,** 187-193.

Spaak J.W., Baert J.M., Baird D.J., Eisenhauer N., Maltby L., Pomati F., Radchuk V., Rohr J.R., Van den Brink P.J. & De Laender F. (2017) Shifts of community composition and population density substantially affect ecosystem function despite invariant richness. *Ecology Letters,* **20,** 1315-1324.

Sparks R.E. (1995) Need for ecosystem management of large rivers and floodplains. *BioScience,* **45,** 168-182.

Stanford J.A., Ward J.V. & Liss W.J. (1996) A general protocol for restoration of regulated rivers. *Regulated Rivers: Research and Management,* **12,** 391-413.

Stubbington R., Wood P.J. & Boulton A.J. (2009) Low flow controls on benthic and hyporheic macroinvertebrate assemblages during supra seasonal drought. *Hydrological Processes,* **23,** 2252-2263.

Thornbrugh D.J. & Gido K.B. (2010) Influence of spatial positioning within stream networks on fish assemblage structure in the Kansas River basin, USA. *Canadian Journal of Fisheries and Aquatic Sciences,* **67,** 143-156.

Timus N., Czekes Z., Rákosy L. & Nowicki P. (2016) Conservation implications of source–sink dynamics within populations of endangered *Maculinea* butterflies. *Journal of Insect Conservation,* **21,** 369-378.

Townsend C.R. & Crowl T.A. (1991) Fragmented population structure in a native New Zealand fish: an effect of introduced brown trout. *Oikos,* **61,** 347-354.

Turner M.G. (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology, Evolution, and Systematics,* **20,** 171-197.

Vander Zanden M.J., Hansen G.J.A. & Latzka A.W. (2017) A framework for evaluating heterogeneity and landscape-level impacts of non-native aquatic species. *Ecosystems,* **20,** 477-491.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences,* **37,** 130-137.

Vitousek P.M., D'Antonio C.M., Loope L.L. & Westbrooks R. (1996) Biological invasions as global environmental change. *American Scientist,* **84,** 468-478.

Vörösmarty C.J., McIntyre P.B., Gessner M.O., Dudgeon D., Prusevich A., Green P., Glidden S., Bunn S.E., Sullivan C.A., Reidy Liermann C. & Davies P.M. (2010) Global threats to human water security and river biodiversity. *Nature,* **467,** 555-561.

Ward J.V., Tockner K. & Schiemer F. (1999) Biodiversity of floodplain ecosystems: Ecotones and connectivity. *Regulated Rivers: Research and Management,* **15,** 125-139.

Weaver W. & Shannon C.E. (1949) *The mathematical theory of communication,* University of Illinois, Urbana, Illinois.

Wickham H. (2009) *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Wilcox K.R., Tredennick A.T., Koerner S.E., Grman E., Hallett L.M., Avolio M.L., La Pierre K.J., Houseman G.R., Isbell F., J.N., Robinson C.H., Sala O.E., Smith M.D., Soudzilovskaia N.A., Souza L., Tilman D., White S.R., Xu Z., Yahdjian L., Yu Q., Zhang P. & Zhang Y. (2017) Asynchrony among local communities stabilises ecosystem function of metacommunities. *Ecology Letters,* **20,** 1534-1545.

Winterbourn M.J., Rounick J.S. & Cowie B. (1981) Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research,* **15,** 321-328.

Wohl E., Angermeier P.L., Bledsoe B., Kondolf G.M., Mac-Donnell L., Merritt D.M., Palmer M.A., Poff N.L. & Tarboton D. (2005) River restoration. *Water Resources Research,* **41,** 1-12.

Woodford D.J. & McIntosh A.R. (2010) Evidence of source–sink metapopulations in a vulnerable native galaxiid fish driven by introduced trout. *Ecological Applications,* **20,** 967-977.

Woodford D.J. & McIntosh A.R. (2011) Location of demographic sources affects the distributions of a vulnerable native fish in invaded river networks. *Freshwater Biology,* **56,** 311-324.

Woodford D.J. & McIntosh A.R. (2013) Effects of introduced trout predation on non-diadromous galaxiid fish populations across invaded riverscapes. *Science for Conservation,* **320,** 1-23.

Woodward G., Perkins D.M. & Brown L.E. (2010) Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society of London: Biological Sciences,* **365,** 2093-2106.

Young R.G. & Hayes J.W. (2004) Angling pressure and trout catchability: behavioural observations of brown trout in two New Zealand backcountry rivers. *North American Journal of Fisheries Management,* **24,** 1203-1213.

Zeileis A., Kleiber C. & Jackman S. (2008) Regression models for count data in R. *Journal of Statistical Software,* **27,** 1-25.

Zeni J.O. & Casatti L. (2014) The influence of habitat homogenisation on the trophic structure of fish fauna in tropical streams. *Hydrobiologia,* **726,** 259-270.